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ADVANCES IN AGRONOMY

VOLUME VI

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AGRONOMY

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VOLUME VI

Edited by A. G. NORMAN
University of Michigan, Ann Arbor, Michigan

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Preface

Man must eat. Of all occupations the production of food is the most basic. Through advances in our knowledge of soils and soil management, and crop plants and crop husbandry, food production in much of the New World, and in most other countries where scientific agriculture is practiced, keeps in step with the requirements of ever-expanding populations. This is the achievement of professional agronomists, and the accomplishment by which their science may be judged. Their very success may make for certain economic complications, which may lead to controls, quotas, subsidies, price supports, and stockpiles, some of which in turn rebound in influence on production methods and land use. A guaranteed crop price may cause an increase in the acreage planted; acreage limitation on the other hand may put a premium on rapid adoption or intensification of newer practices which may increase acre yields. Economic questions do affect the direction of development of agronomy, just as agronomic progress and its adoption affect the whole agricultural economy.

In those great areas of agricultural deficiency and accompanying food inadequacies, much could be accomplished by acceptance and adoption of practices found worthwhile elsewhere. Although local circumstances may affect the direct applicability of methods and materials developed elsewhere, basic knowledge is an international currency that is of world-wide value.

It is the function of this series to review progress in basic research in soil and crop science and developments in agronomic practice. As indicated in earlier volumes, the central theme is soil-crop relationships, but in the selection of material the editors do not restrict their choice only to papers dealing with the conventional subdivisions of soil and crop science, but prefer to be guided by the consideration of usefulness to the professional agronomist.

This volume follows the general pattern of its predecessors. In view of the attention now centered in the provision of aid and advice in the improvement of agricultural practices in less developed countries, the article by Harrar is particularly pertinent. In it he recounts the principles which have been followed by the Rockefeller Foundation in their highly successful programs in Central America. On the domestic scene, Savage and McIlvain review the great changes that have been brought about in range improvement as a result of the application of basic agronomic principles to range problems. Wilsie and Shaw take a broad viewpoint and discuss the adaptation of crops to environment and the influence of climatic factors on problems of crop production. Their examples are mostly taken from North American experience, but the information summarized is an example of that currency that is international.

A. G. NORMAN

Ann Arbor, Michigan
July, 1954

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Progress in Range Improvement

E. H. McILVAIN AND D. A. SAVAGE

U. S. Department of Agriculture, Woodward, Oklahoma[*]

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[*] Including investigations on the U. S. Southern Great Plains Field Station, Woodward, Oklahoma; of the Forage and Range Section, Field Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture, in cooperation with the Animal and Poultry Husbandry Research Branch, the Production Economics Research Branch, the Soil Conservation Service, and the Oklahoma Agricultural Experiment Station.

I. INTRODUCTION

Attention to improving the range lands of America has fluctuated greatly within the last 60 years, mainly as a result of periodic reversals in climatic conditions and shifting public sentiment with regard to land use policies. Major interest in the subject was first aroused late in the nineteenth century when a cataclysmic drought and attendant overgrazing caused widespread destruction of range forage resources. Public recognition of this problem resulted in financial aid for establishing grass-improvement stations by the United States Department of Agriculture at several locations in the West, including Abilene and Channing, Texas, Garden City, Kansas, and Walla Walla, Washington.

This early interest in grassland research and improvement in America is further indicated by the fact that Circular No. 1, the first such publication by the United States Department of Agriculture, and several subsequent publications, were on the subject of grass. This initial work was conducted by the old Division of Agrostology, a forerunner of the present Section of Forage Crops and Diseases. Several valuable grasses were introduced and tested during this period, including crested wheatgrass, *Agropyron cristatum*, the King Ranch strain of Turkestan bluestem, *Andropogon ischaemum*, and weeping lovegrass, *Eragrostis curvula*. Considerable attention also was devoted to grazing management as affecting range land development.

If these early range investigations had been continued and supported on a sound basis through the years, they would undoubtedly have yielded much valuable information of the kind so badly needed in more recent times. Unfortunately, however, public interest in cultivated crops discouraged grass research, eliminated financial support for it, and resulted in its virtual discontinuance near the beginning of the present century. Thereafter a relatively static period of inaction in grassland improvement prevailed until about 1930. Many of the earlier introductions of exotic grasses were lost during this period. However, the interval witnessed a few notable studies by outstanding investigators and early botanists, including those of Jared G. Smith, N. E. Hansen, A. W. Sampson, David Griffiths, J. J. Thornber, J. E. Weaver, F. E. Clements, J. S. Briggs, H. L. Shantz, W. R. Chapline, and J. T. Sarvis.

The Great Drought of the 1930's again focused public and private attention upon the importance of grasslands and their critical need for improvement. The result has been greatly expanded research, education, extension, and positive action on many phases of grassland development, management, and utilization throughout the range lands of America. Much valuable information has been developed by research and action agencies and successfully applied by leading stockmen. However, it must be admitted that there remains a great dearth of precise factual information for solution of many highly complex and variable problems which prevail in the range country.

It has been conservatively estimated that complete application of currently available information on range management by stockmen of the West and South could easily double present grazing returns from the land. Increases of greater magnitude would be possible through further intensive research for development of more factually complete information on all phases of range improvement, plant development, and livestock management.

These and related phases of improvement are encompassed by the term "range management," which is being adopted throughout the West to cover the science, theory, and art of grazing land development and management. Many past recommendations on the subject have been based largely on theoretical principles rather than proved facts. Range management can be expected to become more of a science with future acquisition of more factual information.

In its original concept, management of ranges or pastures referred merely to the manner in which livestock were handled on grazing lands. The term has assumed increasingly broader and more comprehensive significance through the years. Range management was defined by Stoddart and Smith (1943) as "the science and art of planning and directing range use so as to obtain maximum livestock production consistent with conservation of range resources."

Proper range management assumes many specific aspects. It includes adequate development and wise use of improved range lands. It entails revegetation of depleted areas, establishment of sown or reseeded pastures, and construction of adequate facilities for retaining, spreading, and impounding water. It provides for control of troublesome plant, insect, and animal pests and fire. It entails appropriate attention to all phases of animal husbandry, including the best class of livestock during proper seasons and the integrated use of growing and harvested feeds as well as minerals and other supplements. It also takes into account the co-ordination and relationship of grazing with other forms of land use, including timber, water, big game, and recreation.

Grasslands of the United States embrace about 1052 million acres or more than one-half of the total area. Most of this lies in the West, although an extensive area of new grazing land is being developed in the South. The 17 western states support over 25 million cattle, 32 million sheep, and several million big game animals. The area contains about two-thirds of the nation's cattle and about three-fourths of the sheep population.

The purpose of this paper is to present developments in the comparatively new science of range management, emphasizing its importance, showing progress of research, and expressing the author's viewpoints on the subject.

II. GRAZING MANAGEMENT

Range lands of America are located mostly in dry areas where forage yields are low and economical use of intensive practices is more limited than in humid regions. However, the potential for percentage improvement appears to be equally great in both areas. Some form of grazing management, involving the controlled use of livestock, offers the greatest possibility for improving most of the western ranges, with the more intensive practices applicable to favored sites. Several noteworthy developments have occurred in recent years in both of these major fields of approach.

1. Some Basic Concepts

A discovery of first magnitude was that grass requires protection from continual close use during the growing season. Early settlers failed to recognize this important principle. Bentley (1898) vividly described conditions and range philosophy in the early days of settlement near Abilene, Texas:

> The general collapse came in 1884, when the stockman who was not financially ruined was the exception. By that time the range also was about ruined, and whereas ten years before its capacity for maintaining cattle was perhaps 500 cows to every square mile, this capacity had been diminished, as a result of bad management, until 10 acres to a cow were necessary.

Bentley further stated that, in a meeting of stockmen in the vicinity of Abilene, a discussion was held concerning the failing range conditions. Good-natured arguments ensued as to what grasses grew on the range, and it was obvious that none of those present knew anything about them. This philosophy of the ranchers was well shown by this solution to their problem:

> Resolved, that none of us know, or care to know, anything about grasses, native or otherwise, outside of the fact that for the present there are lots of them, the best on record, and we are after getting the most out of them while they last.

It is now well known by ranchers that grass manufactures food in its leaves, which in turn helps develop vigorous roots essential for production of bountiful forage. This knowledge has encouraged stockmen to leave a substantial reserve of unused forage on the land during the growing season.

Another basic principle of range management—the importance of maintaining a surface covering of living and dead vegetation to increase water intake and control erosion—was substantiated by Ellison (1944). Using a high-speed camera to study raindrop action in relation to soil movement, he determined that micro-soil-movement, the forerunner of erosion, was caused by individual raindrops striking unprotected soil surfaces. The impact of a single raindrop caused soil particles to be thrown as high as 2 ft. into the air. Soil disturbed in this manner was transported easily by runoff water.

Borst and Woodburn (1942) showed that a surface mulch was more effective in preventing runoff and erosion than was any type of cultivation. Duley and Domingo (1949) found that intake rate of water into the soil depended largely upon percentage protection of soil surface rather than on kind of vegetation or type of soil. Osborn (1952), working with a portable rain-making machine in the southern Great Plains, found that very sandy soil without vegetative covering was soon sealed over by "fines," with resultant impermeability. It was also determined that slope is a major factor in amount of erosion on cultivated land, but well-grassed soils may have very little erosion on slopes of 20 per cent or greater.

It is desirable to have a complete covering of litter or growing vegetation on the soil. However, range managers have not ascertained the extent to which it is economically possible to leave ungrazed forage to provide this soil covering.

2. Proper Stocking Rate

Proper rate of stocking is probably the most important information needed by range operators. Unfortunately, such information is difficult to determine.

The procedure used to ascertain carrying capacity during the period 1910 to 1930 consisted of ocular estimates of percentage density (ground cover) of grass, forbs, and shrubs. Arbitrary factors, called "palatability ratings," "forage acre factors," and "forage acre requirements" were then decided upon, usually around a conference table, and used to convert the figures for vegetational density into carrying capacity. This system was largely discontinued during the 1930's, because it was unreliable.

In recent years, other approaches have been used to determine proper stocking rates. The more reliable but likewise more expensive method is use of controlled grazing experiments with differentially stocked ranges. The other method involves use of ecological principles to determine range condition and trend so that inferences can be made as to proper use by studying effects of past use.

a. Grazing Experiments. Grazing experiments have not been wholly satisfactory for determining proper stocking rates. It has been found necessary to conduct long-time studies which must encompass climatic extremes typical of the region. These conditions have rarely occurred to date in areas where the grazing studies have been conducted. Moreover, objectives of some of the grazing trials have been to demonstrate the evils of overuse rather than to determine proper use. Consequently, results of grazing trials have often been disappointing and conflicting.

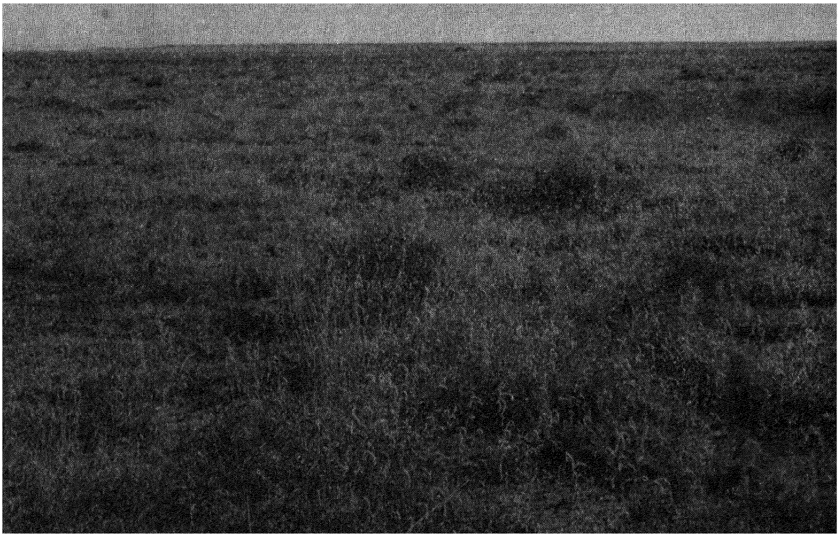

FIG. 1. Short-grass range grazed for four years, May 10 to November 10, at the rate of 40 head of cattle per section. The sod has improved from a fair condition to a good condition, and a desirable mixture of perennial weeds and shrubs provides a balanced diet for grazing animals. Cattle made average gains of 267 pounds on this pasture during the 1946 grazing season. Central Plains Experimental Range, Nunn, Colorado. Photo by U. S. Forest Service.

Clarke *et al.* (1947) conducted a 12-year grazing study near Manyberries, Alberta, Canada. Experimental cattle were grazed at 20, 30, and 40 acres per head for a seven-month season, April through October. Their conclusions were that the 20-acre rate was detrimental to the vegetation. Unused forage at the end of the grazing season on this pasture was less than 25 per cent of the total. They considered the 30-acre rate to be moderate grazing wherein about one-third of the total production remained unused at the end of the grazing season.

A grazing study at the Central Plains Experimental Range near

Fort Collins, Colorado, on short grass similar to the range at Manyberries, showed the necessity of leaving about 50 per cent of the forage unused at the end of the growing season to obtain moderate usage (Costello, 1944) (Figs. 1 and 2).

Grazing results on sand sagebrush, *Artemisia filifolia,* range at Woodward, Oklahoma (McIlvain and Savage, 1950), showed that pastures with 10 to 15 per cent of the grass remaining unused at the end of the yearlong grazing period (about April 15) suffered no ill effect and made more beef and net profit per acre during a ten-year period than did pastures which had 25 per cent of the forage remaining.

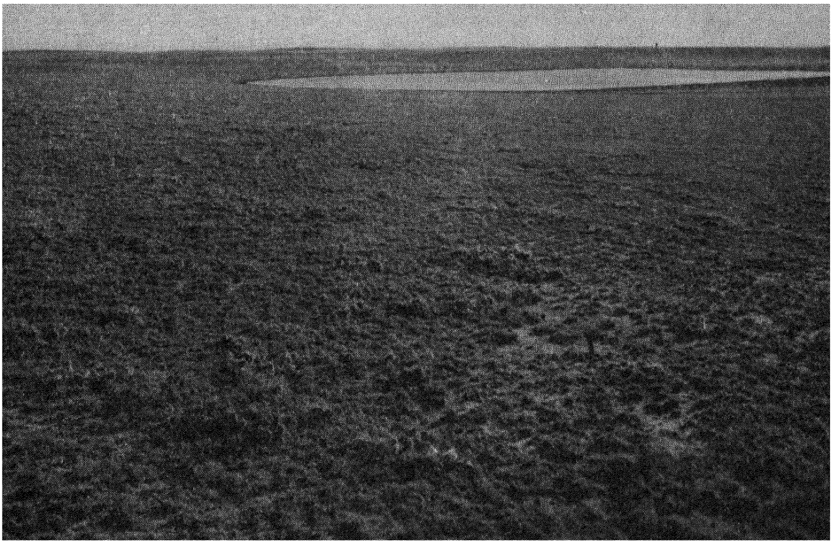

FIG. 2. Short-grass range grazed for four years, May 10 to November 10, at the rate of 60 head of cattle per section. The sod is gradually breaking up, palatable weeds have practically ceased to exist, and the shrubs (both palatable and unpalatable) have disappeared. Cattle made average gains of 126 pounds on this pasture during the 1946 grazing season. Central Plains Experimental Range, Nunn, Colorado. Photo by U. S. Forest Service.

Readers are cautioned to avoid direct comparisons of the results at Woodward with those at the other two locations, because range conditions were decidedly different and the reported reserves of unused forage were recorded at different times in the year. Yearlong grazing is practiced at Woodward, whereas only summer-long grazing is used near Fort Collins and at Manyberries, with forage reserves determined near the end of the winter dormant period in the former case and at the end of the growing season in the latter instances. Yearlong grazing requires conservative summer use, since sufficient vegetation must remain on the ground in the fall to carry livestock until spring growth commences. The soil at Woodward is a deep sand compared with a heavy loam soil at the other two locations. The vegetation at Woodward consists of an upper story of sand sagebrush, with a productive stand of tall, mid, and short grass as an under story. Nearly pure stands of short grass are the dominant vegetation at Fort Collins and Manyberries. Annual forage production averaged about 1500 pounds of air-dry material per acre at Woodward, about 800 pounds at Fort Collins, and about 300 pounds at Manyberries.

There is another important difference between conditions at Woodward and those at the other two stations. Annual production of sand sagebrush herbage at Woodward was also about 1500 pounds of air-dry herbage per acre. Sand sagebrush is a semipalatable shrub which is grazed by choice only during late winter, except under emergency conditions of drought or other forage shortage. When the cattle at Woodward ran out of grass at the heavily grazed rate, which they did in some winters, they subsisted on sagebrush. Much of the annual production of sagebrush foliage is left as litter to help prevent soil erosion and serve as a source of organic matter.

Woolfolk and Knapp (1949) reported on an eight-year range-stocking experiment with Hereford breeding cows at the United States Range Livestock Experiment Station near Miles City, Montana. Heavy stocking during the suckling period retarded the growth of range calves as much as 33 pounds per head compared with moderate and light stocking. Calves removed from heavily stocked range failed to recover from this effect during the winter when fed hay free choice or during the following summer when grazed on lightly stocked range.

Sarvis (1941) conducted a 25-year grazing study in western North Dakota on short- and mid-grass range consisting of blue grama, *Bouteloua gracilis*, western wheat, *Agropyron smithii*, nigger wool, *Carex filifolia*, and needle-and-thread grass, *Stipa comata*. He stated that 20 to 25 per cent of the vegetation should remain on the land at the end of the grazing season for moderate use.

Much work has been done on grazing intensity of spring-fall ranges of the Intermountain Region. Although seasonal use was the primary consideration here, it was important also to determine proper grazing intensity. Craddock and Forsling (1938) found that 80 per cent removal in fall was not detrimental to the range. They further stated that one-third of the vegetation could be taken in spring and one-third in fall without injury on a long-time basis.

b. Determining Range Condition and Trend. Talbot (1937) was among the first to use the range condition approach to carrying capacity determinations. He stated that there were indicators or "signs on the ground" to range happenings. Advanced stages of improvement or decline were usually unmistakable, but range examiners must be able to detect first stages of gradual trends in either direction. This requires keen observation and experience. Indicators are related not only to forage and its condition but also to soil, topography, and climate. He stressed that a single indicator is only one witness; testimony from all possible witnesses should be considered before a verdict is rendered.

Talbot listed as signs of deterioration the following characteristics: pale color, reduced height or volume, close grazing of inferior forage species, thinning plant density (dying out of disintegrated tufts), shrubs resembling trimmed hedge plants, replacement of good forage plants with poor ones, distinct increase of recent gullies and failure of vegetation to invade very small gullies. He listed, as faulty indicators, areas denuded for some reason other than grazing, poisonous plants, condition of annuals, and condition of timber reproduction. His signs of satisfactory use included vigorous appearance and thick stand of forage, absence of accelerated erosion, lack of extensive areas of unpalatable plants, slight or no use of unpalatable plants, absence of serious injury to timber reproduction, reclamation of gullies by vegetation, absence of dead tufts of forage, absence of seedlings of unpalatable plants, at least 20 per cent of seed stocks left unused, at least 25 per cent of the forage of more palatable species and 50 per cent of the less palatable left unused, and unpalatable plants left ungrazed.

Ellison *et al.* (1951) stated that range condition is the characteristic of a vegetal cover and the soil, under grazing use, in relation to what it ought to be. A range is a complex made up of parts so closely interrelated and normally so well integrated or adjusted to one another that what affects one affects all. These parts can be grouped in five classes—animals, vegetation, soil, climate, and topography. Condition is the status of the range; trend is the way that status is changing; and utilization is one of the most important causes of trend and hence ultimately of condition. They stated that stable soil is a prerequisite to satisfactory condition and that loss of vegetation results in loss of soil, the basic resource.

Costello and Schwan (1946) have described how to determine condition and trend on Ponderosa pine ranges in Colorado. The principle of their method is the same as that of the foregoing authors. They stated that trend can be upward, downward, static, or not apparent. Humphrey (1945) pointed out that classification of range condition is basically related to a classification of site. Dyksterhuis (1949) reasoned that plant vigor is an indication of trend and not condition. Sampson (1949) emphasized that the procedure presupposes intimate local information of the whole range complex.

Parker (1951) developed a three-step method of determining trend in range condition. The method combined periodic measurements with extensive, wide-scale estimates on density, floristic composition, vigor, litter, soil capabilities, and erosion features on replicated and permanently located plots. The technique was widely tested on national forests throughout the West and was found to be rapid, accurate, sensitive, and relatively simple. Step one consists of collecting basic field data from permanently established quadrats. Step two consists of analyzing these data in the field, classifying condition, and estimating range trend. Step three is a permanent photographic record of range conditions.

Although determination of range condition and trend is conceded by many to be the most practical method of establishing proper use, many theories on which it is based have not yet been corroborated by precise investigations. Limited investigational work has shown that the highest ecological condition of vegetation is not always most productive for livestock.

In studies conducted on short-grass pastures in northwestern Kansas, Tomanek (1948) found more moisture available for plant growth under moderate grazing than in underutilized or overutilized pastures. The moderately grazed areas had enough litter and debris to cover the few bare spaces, and they were utilized sufficiently to retard excessive transpiration. The cover of perennial grasses on moderately grazed pastures was nearly twice that on other pastures. The highest seasonal yield of short grass in pounds per acre was produced on moderately grazed pastures followed in order of their yields by undergrazed, ungrazed, overgrazed, and heavily grazed locations.

The ungrazed location contained slightly over 1 ton of litter per acre, followed by 1800 pounds in the undergrazed, 730 in the moderately grazed, 49 in the overgrazed, and 30 in the heavily grazed pasture. This study indicates the value of litter determinations as a guide to proper use.

c. Distribution of Grazing. The range manager, technician or stockman, often goes to great lengths to determine proper stocking rate for a given range. He correctly uses feed measurements, past history, and estimations based on similar ranges to provide a seemingly sound basis for his determination. Too often the range manager overlooks the matter of distribution of grazing, which may be the factor governing whether an estimated carrying capacity is proper or improper.

Valentine (1947a) pointed out several instances of great discrepancy between grazing capacity as determined by range survey and actual stocking. The survey error was made in assuming uniform utilization of vegetation rather than a graduated reduction in use as distance from water increased. A pasture on the Jornada Range in southern New Mexico was surveyed and calculated to have a conservative grazing capacity of 137 animal units, but it was actually overgrazed with 112 units. Valentine stated that the quantity of vegetation is not the usable index to stocking rate, since accessibility of forage is directly dependent on its distance from water Several other range investigators in the West have corroborated these findings.

Factors used to obtain proper distribution of grazing include stock water developments, fencing, riding or herding, salting, feeding supplements on underutilized areas, and furnishing shade in summer and shelter in winter. The most important of these factors is water development.

Location of water helps to control movement, distribution, and concentration of livestock. Inadequate stock water development prevents profitable utilization of badly needed grazing areas and encourages destructive overgrazing in the vicinity of existing water supplies (Hamilton and Jepson, 1940). In addition to natural sources, water can be provided by wells, reservoirs, springs, pipelines, and hauling. All applicable facilities of this kind should be developed to the greatest economic extent on every ranch.

Short drift fences, strategically placed across waterways, can be used to control grazing and deflect livestock from creek bottoms to hillsides for more uniform use. Different vegetative types can often be more fully utilized by fencing them separately (Miles, 1951). It is sometimes desirable to cross-fence a range so that livestock will utilize less attractive areas where they would not normally graze.

On large open ranges, riding or herding is often the only feasible means of controlling livestock distribution. This method is not used so widely as it should be in many localities, chiefly because of the belief that it is a costly practice. Actually the practice would pay in many instances by saving supplemental feed required in winter or drought periods.

Placement of salt has long been recognized as a valuable method to attract animals to underutilized areas. For various reasons many operators fail to utilize this technique, and livestock are habitually salted at the watering places.

Supplemental feed in the form of hay or protein concentrate can be used effectively to attract animals into underutilized areas. Since pickup trucks and jeeps are now widely used to feed livestock, there is little need to feed them at their watering place. Salt-meal feeding, wherein salt is used to control daily consumption of protein supplements, offers a convenient means of distributing livestock.

Some ranges can take advantage of placement of artificial shade in the summer and shelter in the winter to attract livestock to obtain more uniform distribution of grazing. It has been determined that livestock will seek out these favorable environmental locations. Ultimate development of this technique would provide for movable installations.

3. *Proper Class of Livestock*

It is extremely important that the proper class of livestock, *i.e.*, cattle, sheep, or goats, utilize range vegetation to which they are best adapted. Goats use much browse, a fair amount of weeds, and only a little grass, whereas sheep graze forbs, grass, and brush in that order of preference. Cattle prefer grass, forbs, and browse in descending order (Fraps and Cory, 1940). It is unwise to graze cattle predominantly on browse range or to graze goats on pure stands of grass.

Range managers are finding that multiple use by several classes of livestock is preferable to use by a single class in some instances. Long-time rotations may become feasible, *i.e.*, after cattle use a range for several years, forbs and browse become more abundant and the range becomes better adapted for sheep or goats. Similarly, constant use by sheep or goats tends, in some instances, to decrease forbs and browse and increase grass so that the range becomes better adapted for cattle.

The geographic range of profitable cattle raising has been extended southward in the United States by crossbreeding English and Brahman breeds, the cross being known as Braford for the Brahman-Hereford cross, Brahorn for the Brahman-Shorthorn cross, and Brangus for the Brahman-Angus combination. The Santa Gertrudis breed is a well-known and well-developed example of the Brahman-Shorthorn cross. Rhoad and Black (1943), working in the South, recommended breeding Brahman hybrid beef-type bulls to range cows which contain one-half to three-fourths the blood of a pure beef breed. One parent of the hybrid bulls should be of the same pure beef breed that sired the range cows and the other parent predominantly of Brahman breeding and of acceptable beef-type conformation.

Cattle raising has been extended northward on the continent by hybridizing English breeds with buffalo, the cross being known as "cattalo." A herd of about 150 cattalo cows is being increased at the Dominion Livestock Experimental Range near Manyberries, Alberta, Canada. Only about 25 per cent of the first cross are fertile, and needless to say, many of them are extremely odd looking creatures. However, they are growthy, show beef-type characteristics, and most important, can endure severe winter weather, as indicated by past experience with the herd at Wainwright, Canada. The third and fourth filial generation lose the external characteristics of the buffalo with the exception of total size and a slight hump.

4. Proper Season of Use

Much western range land is grazed yearlong, and determination of proper season of use offers little as an improvement practice. Other ranges, particularly those adjacent to or in mountainous areas, must be used seasonally because of weather conditions.

Early spring grazing is known to be extremely detrimental to forage plants. Recent investigations have shown, however, that heavy fall grazing when the plant is building up its root reserves can be as detrimental, or even more so, than spring grazing. Ranges vary in this characteristic, and the pertinent facts must be determined by investigations in each major area.

Mueggler (1950) studied the relative effect of fall versus spring-fall grazing on sagebrush-grass range near Dubois, Idaho. After 25 years of treatment, areas that were originally similar differed greatly. Heavy fall stocking did not markedly affect areas in good condition. However, the ecological condition of areas grazed in both spring and fall changed from good to poor. Heavy spring stocking severely reduced grass and forb production and greatly increased the abundance of undesirable shrubs.

Some investigational work has been done on correlating weather and plant development data as determinants of grazing periods on mountain ranges. Costello (1939) reporting on a 10-year study at the Great Basin Branch Station, Ephraim Canyon, Utah, found that rate of snow disappearance was related not only to beginning of active growth but to plant development during the entire growing season. A reliable forecast for start of spring grazing could be made from date of snow melt. He also determined that opening of the grazing season should be 10 to 14 days later for each 1000-ft. increment in elevation. The start of active growth of grasses, as well as date of range readiness, varied as much as 45 days from one year to the next.

5. Rotation Grazing

It is sound logic to defer grazing of grass so that top growth may be produced to build roots and increase plant vigor. Therefore, it would appear feasible to devise a system of rotation of deferment and use for improved forage production. However logical these aims may seem, they have not been attained experimentally at many points in western United States unless the rate of stocking has been reduced simultaneously. In this connection, the discussion is here limited to the division of a native range into several parts and the rotation of livestock from one part to the others at intervals during the grazing period.

In an investigation of rotational use of a bunch grass in eastern Oregon, Sampson (1913) found that rest was needed to enable plants to regain sufficient plant vigor to produce seed. A period of grazing was then found desirable to disturb the soil and plant the seed, after which another rest period promoted seedling establishment.

Jardine (1915) devised a three-pasture system of rotation based on Sampson's findings and on work in New Mexico. The principle was to graze one pasture for about two months in the spring, another division the next two months, and the third division the last two months of the growing season. This plan was to be followed two successive years, and then the rotation was to be changed to spring-protect another division for two successive years. This system was based on logic, but it was not precisely tested. It was rather commonly accepted as an improvement practice by many early range managers. Subsequent studies have not shown this principle to be widespread in application.

Inherent in any rotation scheme is a period of abuse as well as a period of rest. It seems that the detrimental effects of heavy stocking may be greater than the beneficial effects of light stocking in many instances. Some recent workers have used this principle to devise new rotation schemes, according to an informal report by J. D. Scott of South Africa. Their plans provide for grazing heaviest during the season when rest is not needed, applying less grazing pressure or more deferment at other times.

Rogler (1951) reported results of a 25-year comparison of continuous and rotation grazing in the northern Plains. A three-division, standard, Jardine-type rotation was compared with continuous grazing. Two-year-old steers were used for the first 17 years and yearling steers for the last 8 years. The two-year-old steers averaged 34.8 pounds more gain per head per season on the rotation pasture than on the continuously grazed pasture. However, the yearling steers gained 20 pounds more per head under continuous grazing than under rotation grazing. Rogler believes that the wide difference shown by the two classes of animals was due to the greater ability of two-year-old steers to utilize the coarse forage which accrues under a rotation system on dry-land range. He and his predecessor, J. T. Sarvis, concluded that continuous moderate grazing was superior to rotation grazing. However, the vegetation was benefited slightly by rotation use in this study.

McIlvain and Savage (1951) conducted an 8-year study of continuous grazing compared with rotational grazing at both heavy and moderate stocking rates on the Southern Plains Experimental Range near Woodward, Oklahoma. The rotation system used at the start of the study was the type employed in the northern Great Plains. Gains of yearling steers were reduced 65 pounds per head by rotation grazing at the heavy rate and 37 pounds at the moderate rate during the first summer. Effects of these rotations on the grass was very detrimental. The system was changed during the next 5 years of the study to provide for rotation at monthly intervals. Continuous grazing during this period resulted in a 7 pound per head advantage over rotation grazing at the heavy rate and 9 pounds at the moderate. Since monthly rotation resulted in less gain reduction to livestock, rotation was made semimonthly for the next 2 years of the study. There was no difference in steer gains between the two systems at the heavy rate, whereas a slight advantage still remained for continuous use at the moderate rate.

In the Woodward study the vegetation was benefited slightly by rotation grazing, particularly at the heavy stocking rate. Improvement was striking in the center division of each three-division pasture. It was impossible to determine the cause of improvement on this pasture division and to ascertain the lack of improvement on the other two divisions. A fortunate coincidence of lack of grazing pressure, favorable weather conditions, and seedling establishment must have been responsible.

It took 8 years to effect this noticeable improvement on one-third of each rotation pasture. One might assume that in another 8 years two-thirds of the pasture might be materially benefited and that at the end of a 24-year period the entire pasture might be improved. It is true that a quarter of a century is a short period of time in the ecological and economical life of western range. Therefore, it might be assumed that in the course of many years this type of rotation would be beneficial, particularly at a heavy rate of grazing. Facilities for fencing, watering, and moving the livestock need to be considered in the economics of the practice.

Black and Clark (1942) reported on a 4-year rotation grazing study at Ardmore, South Dakota, under yearlong grazing with cattle rotated every 28 days. They concluded there was no difference in cattle weights or vegetation due to either system of grazing. They had found an advantage from rotation grazing in an earlier study.

It is common knowledge that grasses lose moisture in winter, but recent studies reveal that they also lose from 25 to 33 per cent of their air-dry weight from the time of maximum development in mid-summer to the first frost. This fact, when more fully understood, promises to lead to new principles of ranch management in this region.

Turner and Klipple (1952), working on short-grass range in northeastern Colorado, stated that reductions of over 30 per cent of the maximum herbage weights of blue grama were observed during late summer and fall. Additional losses occurred during winter. Causes of decline in herbage weights were not investigated; however, they stated that translocation, leaching, and oxidation may be important factors. They also determined that there was little loss from leaves being broken off or blown away, and the reduction in weight occurred whether or not seed stalks were produced. They found that harvesting blue grama vegetation to the root crown once during the growing season and again in October removed a greater total weight of air-dry herbage than harvesting only in October. The implication of these findings is great when one realizes that blue grama furnishes three-fourths of the native forage supply in eastern Colorado.

Unpublished data obtained at Woodward, Oklahoma, supports the work of Turner and Klipple. A total of 218 pounds of herbage out of 1034 pounds was lost from native range exclosures protected from large rodent and cattle use during the period September 20, 1950, to April 9, 1951. Similarly, 347 pounds were unexplainably lost from a total of 787 pounds during the period October 19, 1951, to April 1, 1952.

The problem that remains to research is to determine if this loss contributes materially to maintenance of vigor of the plant or fertility of the site. It will be necessary to establish the proportion that is due to chemical action and that due to physical forces.

6. Use of Fire

Fire is a much-disputed factor in range development. The four primary grazing regions which use fire as a range practice are the Flint Hill ranges and Osage grasslands of Kansas and Oklahoma, the brushland ranges of California, the big sagebrush areas of the Intermountain and Rocky Mountain regions, and the Piney Woods areas of the South. Even within these broad regions, there is much controversy over the effect of fire, since it can be beneficial or detrimental depending on how it is used. Much additional research is needed on the subject.

In the Flint Hills of Kansas and the Osage region of Oklahoma, many two-year-old steers from the southwest are fattened for slaughter as grass-fat animals, or as feeder steers which need only a short finishing period. These animals are placed on pasture about May 1 and often are marketed in July or early August. They make excellent live-weight gains, usually between 250 and 300 pounds per head, primarily on burned pastures where grass is lush and plentiful and unencumbered by any residue from the previous year's growth. Southwestern cattlemen usually stipulate as part of their rental contract that the range must be burned. They know from past experience that burning promotes their cattle gains.

Scientists working in that area have determined that annual forage production is reduced 30 to 40 per cent by annual burning. They found least harm was done by burning in late spring or just prior to greening up of the grass (Aldous, 1934). The longer the land remained nude and bare, the more injury occurred to the vegetation, and the more reduction in forage production. Their findings are well known by stockmen of that region; nevertheless, the practice of burning each spring continues. Wayne Rogler of Matfield Green, Kansas, in the heart of the Flint Hill region, sums up the controversial matter this way:

> As a land owner in this region, I would not want my pastures burned; but I would not lease a pasture unless it were burned.

Close to the Osage grasslands of Oklahoma lie the Oak-savanna Plains, where the Red Plains Experiment Station is located. Elwell *et al.* (1941) reported results after eight years of fall burning tall grasses at this station. Burning at that time of year caused a loss of nitrogen, destroyed organic matter, increased both soil and water loss, and reduced grass production from 40 to 60 per cent. They suggested that spring mowing replace burning wherever possible.

Hopkins *et al.* (1948), working in mixed prairie vegetation at Hays, Kansas, reported that the quantity of litter on the ground at the time of burning greatly affected results. On an area covered by light litter, basal cover of grass was still 95 per cent after the fire. On an area covered with heavy litter, cover was reduced to 44 per cent. Western ragweed, *Ambrosia psilostachya*, increased tremendously on the burned range and seriously prevented subsequent recovery of grass. Fall burning benefited wild onion, whereas spring burning damaged this plant.

Big sagebrush, *Artemisia tridentata*, does not root sprout when the top growth is damaged or removed. Pechanec (1944), working in the Intermountain Region, reported that controlled burning of sagebrush, properly planned and executed, increased forage production of perennial grass 100 per cent and perennial weeds 25 per cent. Burning raised availability of forage from 64 to 93 per cent. He stated that approximately four years were required after a burn to bring a range to full productivity. He placed considerations which distinguish planned from haphazard burning in four groups: where to burn, when to burn, how to burn, and how to manage the area after burning. The cost of controlled burning varied greatly between areas but was relatively low, about 20 to 30 cents per acre.

The subject of burning in California has been particularly controversial. Shantz (1947), at the request of the California State Division of Forestry, reviewed all available literature on effect of fire to remove brush. His excellent presentation of the problem included citation of over 500 pertinent references which emphasized the balance between vegetation, soil, weather, and biological factors, and the use of natural vegetation to classify land as to climatic conditions, soil components, and agricultural value.

Shantz pointed out the rise and fall of various past European and Asiatic civilizations that successfully built their agriculture in fertile, irrigated valleys supplied with water from wild mountain ranges. When these watersheds were ravaged by fire and other misuse, they lost their vegetative covering, their soil, and their value to the people. Desert conditions then prevailed over once fertile valleys and mountains, and the populations vanished or became decadent. The one outstanding exception was the valley of the Nile, which is as fertile today as it was 6000 years ago, largely because the headwaters of the Nile are inaccessible to the population of the valley because of the great Sahara Desert.

Shantz emphasized that the primary effect of fire on a site is to make that site drier, and to retard succession, which is continually striving to make a site more moist. He stated:

> Much of the earth's surface now in grassland would without fire surely pass to forests, many coniferous forests would pass to hardwoods, and much of the higher and better part of the Mediterranean type (which includes parts of the California chaparral) would pass to forest. Fire is a part of the environment of this type, and it is maintained by fire—consequently it cannot be removed by fire alone. However, fire carries this type far beyond its natural area.

Shantz emphasized the great need for land planning. Until each plant community is properly classified, it will be impossible to manage the land properly. He summarized by stating that fire can be used as a tool in range management on some sites under some conditions, but it is often harmful under many other conditions.

Adams *et al.* (1947) reported upon a lengthy series of meetings authorized by the California legislature on burning. Eminent and recognized hydraulic engineers, irrigationists, foresters, soil conservationists, ecologists, geologists, and ranchers presented experimental data, facts, figures, and opinions on all aspects of burning. Pertinent excerpts are quoted here because of their excellent summation of the problem.

The viewpoint of foresters who have given especial attention to forest hydrology, concurred in generally by soil conservationists, is that, under natural conditions, the soil, cover, and moisture supply of a watershed tend to be in balance; that plant growth is adjusted to the amount of rainfall, and stream channels to the runoff they must carry. They (the foresters) hold that destruction of the cover decreased the infiltration capacity of the soil and thereby increases the surface runoff, this resulting in increased soil erosion and reduced storage of water in the ground, the latter in turn lessening the sustained flow of the streams.

Soil conservationists, although stressing the role of cover in both water conservation and erosion, seem to have reached the conclusion that grass is fully as effective as other types of cover in preventing soil losses.

Of the engineers whose conclusions have been cited, one denies that forest litter and humus necessarily increase percolation of rainfall into the soil, claiming that if they do have that effect, the increment to ground water is nullified by the excessive transpiration by the vegetation; that forests may absorb and dispose of intermittent showers without permitting any runoff or percolation, while in the open such showers always produce some runoff and contribute to ground water supply; that the net result of these, and other, considerations is that the total runoff from a forested area is less than that from an open one, other things being equal, and that the uniformity of stream flow is not enhanced. Although there are competent engineers who accept the foresters' point of view, the opinions cited are typical of those held by most engineers who have participated in published discussion of this subject.

As to the views of geologists, referring to vegetation, floods, and erosion, they say that when we examine the abundant geological record preserved at many places in our country and extending far, far back of the brief epoch of human occupation, the evidence is quite out of accord with the opinion that there were no serious floods in America before the brief epoch of rapid spread of population, intensive cultivation, and large scale stock raising. Catastrophe is a rule of nature, and we must not lay too much stress upon what is happening today.

The committee concluded that, on the basis of present information, burning can be neither supported nor condemned for all conditions and situations in the California brush and woodland-grass ranges.

7. *Livestock Facilities*

During early days of grazing in the western United States, there were few livestock working facilities except the lariat, a small fire, and a running iron. As conditions became more crowded, the first permanent livestock facility consisted of the barbed wire fence. Today good fences are essential for efficient ranch operation. Many other installations, devices, and conveniences now facilitate handling livestock in the shortest time, at the lowest cost, and with the least harm and loss of animal weight.

Cheaply constructed cement fence posts are now replacing the old wooden posts, which were a never-ending source of concern to the rancher. One type which is giving admirable service is a triangular post about 4 in. wide on each side and 7 ft. long. Three reinforcing rods are included in each post and a pumice stone core is molded into the post along one side so that regular fencing staples may be used.

Another recent innovation in fencing has been psychological rather than mechanical. This consists of attaching common tin cans to electric fences at strategic points where they arouse curiosity of livestock. Cattle are generally not curious about a barbed wire fence, but they are attracted to the strange cans. When their wet noses make contact with the cans, the animals immediately acquire a shuddering respect for the fence!

Development of adequate livestock water is extremely important to a ranch operator. This fact has been recognized for many years, but not to a sufficient degree. For instance, Bentley (1898), in one of the earliest discussions of range improvement methods, stated:

> Dams or tanks can be provided at intervals of 5 miles over the range and all this destruction of valuable pasturage would then be prevented, as cattle would at no time be required to go more than 2½ to 3 miles for water, and they would naturally feed away from water where the best grasses could be found.

Other range managers have recommended maximum traveling distances, usually less than those recommended by Bentley. Hamilton and Jepson (1940) stated that cattle should not travel more than 2 to 3 miles from water on flat, level land and not more than 1 mile in rough terrain. Stoddard and Smith (1943) recommended not more than 2 to 2½ miles for flat land and not more than ½ mile in excessively steep and rough country.

The authors, working with yearling steers in moderately rolling sand dune country near Woodward, Oklahoma, found the back side of small experimental pastures, not more than ½ mile distant from water, to be lightly grazed even in deliberately overstocked pastures. This fact suggests that watering places should not be more than 1 mile apart for most efficient forage use in the southern Great Plains.

This trend toward a closer spacing of watering places is probably very natural when one realizes that the leg length of modern beef cattle is much shorter and the body weight much greater than that of the old longhorn that was used as a basis for early recommendations. It should be the goal of every rancher to increase watering places on his ranch to the point where no animal would have to travel more than ½ mile to water.

Facilities for heating water for beef animals are being more widely used and investigations are only now being conducted to determine the value of the practice. Twenty-four head of heifers on the Southern Plains Experimental Range near Woodward, Oklahoma, were given access to water warmed only during periods of freezing weather during the winter of 1951–1952. These heifers were compared with a similar group treated identically in every respect except for having access to cold water on which the ice was broken daily at feeding time, in accordance with local custom. The heifers having access to warmed water gained an average of 15 pounds more per head during the winter season and maintained this advantage throughout the year.

There has been a rapid development of cattle working facilities for controlling external parasites within the last decade. The dipping vat was first widely used for fly, lice, and tick control. With development of DDT and other insecticides mechanical spray machines replaced the dipping vat.

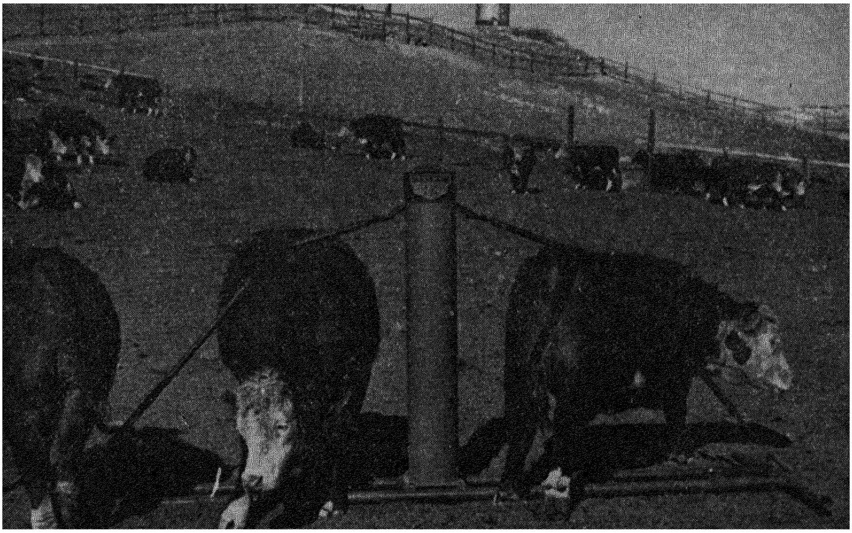

FIG. 3. Feed lot steers using a "rubbing post." A 4-per cent DDT solution in low-grade motor oil rids the cattle of flies in summer and lice in winter.

Now rapidly replacing spray machines are automatic devices which the livestock use themselves to dispense small amounts of insecticide on their itching bodies. These devices are collectively called "rubbing posts," and they are being commercially manufactured by several companies (Fig. 3). Effective homemade rubbing posts can also be made from several strands of old barbed wire, burlap sacks, and a means of support. However, this homemade "post" needs to be treated at approximate 1-month intervals, whereas the commercial machines need be treated only once or twice per year.

An efficient self-sprayer is being made commercially in the Southeast. This machine is generally installed in a gate or other defile so that cattle must pass through it daily. The animals activate a treadle which in turn operates a small, inexpensive, efficient pump that sprays a minute amount of insecticide on the animal. The machine is effective in controlling horn flies, house and stable flies, horse flies, lice, and ticks. It is foolproof in operation and should be a boon to cattle raisers, particularly in the Deep South or Far North, where insect pests are most numerous.

Although new insecticides such as DDT, methoxychlor, lindane, and dieldrin are now doing a miraculous job of controlling cattle parasites, insect populations are rapidly becoming immune and resistant to them; and it is entirely possible that in the foreseeable future resistant populations of each major insect pest will again plague the cattle operator.

Several major improvements have been made in the squeeze systems and working chutes which stockmen use to brand, vaccinate, dehorn, castrate, and doctor their animals. These new chutes, which are being widely used in the livestock industry, enable one man to handle animals weighing from 300 to 1500 pounds. They have ingenious mechanisms for holding each part of the animal immobile and making all parts available to the operator.

The value of shed protection in winter and shade protection during summer for beef cattle has not been well determined. However, a few inconclusive investigations have been made. Research men are becoming more mindful of the potential of these two livestock facilities, and it is probable that their value will be accurately determined in the near future. Ittner and Kelly (1951) reported on a three-year study conducted in the Imperial Valley of California to determine the effect of shade and reduced temperature on gains and health of Hereford and Bradford cattle. Four types of shelters were provided. The most effective was a shed constructed primarily of wire and hay and cooled with a commercial, evaporative, desert cooler. Hereford cattle gained 1.05 pounds per head per day during August and September when given access to this shelter. Two other shelters had double roofs and the lower roof was cooled by water from sprinklers. Hereford cattle gained at the rate of 0.8 pound per head per day under these shelters. The check lot had access to a plain, galvanized, iron-roof shelter. They gained the least—0.6 pound per head per day. It is interesting to note there was no difference in gain of Bradford cattle due to any treatment.

Another facility now widely used by progressive stockmen is the fire guard, a denuded strip of land bordering highways, railroad rights-of-way, and other areas of potential fire danger. Some ranchers are even subdividing their property with fire guards. These fire guards are generally 6 to 12 ft. wide, depending on available machinery. In some localities this guard is not wide enough for complete protection, and the practice has been developed of plowing two guards 50 to 100 ft. apart and burning the vegetation between them.

III. Reseeding

Range reseeding is accomplished by both natural and artificial means. Artificial reseeding offers greater possibilities for range restoration than does natural reseeding. New and more productive grasses can be introduced, it can be done in a relatively short time, and the ultimate goal of establishing legumes in the western range land may have greater possibilities.

Natural reseeding is basically an extremely slow process. The principle of "survival of the fittest," which finally gives climax vegetation, provides that drought resistance, cold resistance, grazing resistance, and longevity take precedence over natural ability to reseed. Nature gives little consideration to factors such as seed production, seedling vigor, or forage production.

1. Scope and Potential

Range reseeding is potentially the most effective means of increasing forage and livestock production on favored sites. Research results indicate reseeding can increase livestock production two- to ten-fold over excellent native range. Literally millions of acres of western range land need to be reseeded to increase production, control erosion, and make them an asset in national economy.

a. Present Status. Reseeding information of a general nature, as well as preliminary guides on specific method of establishment and adapted species, have been reported for the northern Great Plains by Clarke and Heinrichs (1941), Franzke and Hume (1942), and Short (1943); from the central Great Plains by Barnes *et al.* (1950) and Wasser (1950); from the southern Great Plains by Savage (1939), Harper (1947), Nixon (1949), McIlvain and Savage (1950), and Holt *et al.* (1951); from the northern Rocky Mountains by Friedrich (1947) and Killough (1950); from the central and southern Rocky Mountains by Crider (1945), Hull *et al.* (1950), and Doran (1951); from the Intermountain Region by Stoddart (1946) and Stewart (1950); from the Southwestern Desert Region by Bridges (1942), Flory and Marshall (1942), Pearse *et al.* (1948), and Anderson and Swanson (1949); from the Pacific Northwest by Pickford and Jackman (1944) and Stark *et al.*

(1947); and from California by Love (1951, 1952) and Peterson (1951).

Range reseeding has not been developed fully as a range improvement practice, for two reasons. First, there is a dearth of knowledge concerning reseeding methods, adapted species, and proper management of reseeded pastures. Secondly, there is a lack of national need for immediate increase of livestock production. However, since the population of the United States is increasing rapidly, the time is near when increased livestock production will be an absolute necessity.

There is little spare time to commence research on this important subject. An adequate program of research must be inaugurated immediately to determine necessary facts and principles to institute the action program of range reseeding on arid and semiarid land which will be needed in the near future.

b. Problems. Besides lack of immediate need and scarcity of adequate knowledge, there are many pressing problems which deter reseeding. These include lack of adequate seed supplies of adapted strains, lack of consistently effective seeding methods, lack of seeding equipment, lack of seedling vigor, and lack of public education on how to reseed range land.

Many of the factors which comprise an adequate reseeding program are just now being realized. Lacking an aggressive forage plant that can be successfully established in existing vegetation, it is necessary to destroy competing vegetation and prepare a satisfactory seedbed. This is a costly and slow enterprise which probably can be eliminated or rendered less difficult with increased technological development.

Very little is known of use of fertilizers to aid seedling establishment except that application of fertilizer on western ranges at time of seeding generally results in a poorer stand than if no amendment were used. Further studies may show the value of fertilizers in establishment work.

There is also a scarcity of knowledge about control of annual grasses and forbs which often cause complete failure of grass seedings. Much information is needed on management necessary to maintain productivity in reseeded stands. Successful methods have not been developed for establishing legumes on range land. Substantial increase in grassland fertility is dependent on the use of legumes, fertilizers, or both.

c. New Concepts Needed. Most range managers, administrators, and educators have been striving to work with natural forces to increase production. A commonly accepted viewpoint is that the goal of reseeding should be to restore climax vegetation, so that the task will be done correctly, once and forever. This is probably neither possible nor desirable. A new concept is needed by range managers if maximum production is ever to be attained on western range lands.

Climax vegetation in much of the West is a nebulous entity upon which ecologists often disagree. Some hold that grass is climax over vast regions and that moderate or light grazing use will restore productive vegetation. Others maintain that shrubs are climax and that grasslands are maintained by other factors such as fire and grazing, and that moderate or light grazing will increase growth of brush.

Short periods of wide fluctuations in climate occur within a few years, and these periods greatly affect vegetation. Climax becomes an ever-changing entity, explaining some of the disagreement of ecologists as to what constitutes permanent vegetation. These viewpoints have little bearing on the present situation. Future increases in livestock production require wise and efficient use of available resources. Knowledge of ecology can aid this work, but the final procedures must be governed by sound economics consistent with soil stability.

It is not an established principle that climax is the most profitable vegetation on a sustained basis. For instance, cultivated crops in farming sections of the country are far from climax vegetation, but they are usually much more profitable than the original vegetation.

Likewise young reseeded pastures in the East outproduce natural grasslands as much as fivefold. As reseeded stands become old, production usually declines unless a high percentage of legumes is maintained and other forms of renovation used.

It is logical to suppose that many of these principles can be applied to western range lands through development of suitable techniques. In many instances and on favored sites the end result can be replacement of native range with superior production of native or introduced species in sown pastures.

Reduction of organic matter to its elementary components has long been recognized as a vital mineralization process by soil scientists. Only recently, however, has the implication of this knowledge become apparent to range managers. The process is far from being fully understood. A simplified and incomplete explanation of mineralization is that it is a natural process which occurs in arid, hot, short growing season climates; and it has the same end effect as leaching in humid areas, with the exception that fertility passes off as gaseous products instead of being leached deep into the subsoil beneath the depth of roots.

The range management aspects of mineralization have been developed primarily by workers of the British Commonwealth in Australia, Canada, and South Africa. A complete understanding of this process will open greater and wider avenues for development of range management principles. Theron (1951), working near Johannesburg, South Africa, found that living roots repress nitrification. This repression is thought to be due to an antibiotic which paralyzes the autotrophic dehydrogenase system of the nitrifying organisms without interfering with the process of ammonification. He stated that no organic matter can be built up under grass cover unless some extraneous source of nitrogen is provided through legume or fertilizer applications. If his views are correct, and there is good evidence to support them, the ultimate hope of range management must lie in use of legumes, fertilization, or both.

Some British Commonwealth scientists hold that range land fertility is principally due to animal excreta and not to plant residues. Their philosophy is that plant material is most efficiently utilized by livestock, which return 70 to 80 per cent of the nitrate value and much of the other nutrients of the forage to the land. The alternative of this practice is to market the forage as hay or silage or lose it back to the air as products of decomposition—and lose nearly 100 per cent of the fertility. Much of the fertilizer value of legumes is lost when the crop is removed as hay, but it is retained when the plant is grazed and all of the manure and urine left on the land. These statements are confirmed by the work of Karraker (1951).

2. *Recent Developments*

Many new developments in range reseeding have been made since 1940. These preliminary techniques and findings are the foundation for future progress in this field.

a. Principles. Several principles have been developed regarding various phases of reseeding. Presence of big sagebrush on a site indicates that precipitation, temperature, and soils relations are favorable for reseeding and soil salinity is low (Stewart, 1950). Hull and Doran (1950) stated that productive sites should be chosen for initial reseeding trials, because success is more likely there. Savage *et al.* (1948) emphasized the need for adequate seedbed preparation; they advocated establishment of a noncompetitive stubble-mulch cover, usually from sorghums grown the previous year, as an aid in grass establishment by reducing wind erosion, water erosion, crusting, and weed competition. McIlvain and Savage (1950) reported that average profits from growing and grazing a sorghum cover as a preparatory crop paid from one-half to three-fourths the total cost of establishing grass.

It has been determined that grass seeding in weed cover on abandoned cropland generally results in failure, owing to competition from established plants. It has been found that grass must be seeded like other small-seeded crops, including alfalfa. Fall sowings are preferred for cool-season grasses and spring sowings for warm-season grasses. Depth of planting should be shallow, preferably ¼ to ¾ in., because the seeds are small and contain little stored food for initial shoot growth. Rate of seeding depends, of course, upon size and quality of seed. The extremely small-seeded grasses, including sand lovegrass, weeping lovegrass, and sand dropseed, are generally seeded at 1 to 1½ pounds per acre. Grasses having medium-sized seed, such as switchgrass, *Panicum virgatum,* crested wheatgrass, King Ranch bluestem, and Caucasian bluestem, *Andropogon caucasius,* should be seeded from 4 to 6 pounds per acre, and grasses having large or fluffy seeds should be seeded at 8 to 12 pounds per acre.

It was recently discovered that there is a spectacular difference in forage production from southern source seeds as compared with seeds of local or northern origin. Early strain trials made at Woodward, Oklahoma, showed a remarkable step-increase-effect in height growth and forage productivity for strains of grass collected from varying locations in the Plains from north to south. Hopkins (1941) reported similar results for side-oats grama grown at Hays, Kansas. He found that plants grown from Montana seed produced an average of 6 g. of forage per plant; Kansas seed, 16 g.; and Texas seed, 27 g. Other investigators, including the late E. W. Nelson of Colorado A. & M. College, have obtained similar results.

This principle is well established, and it is becoming widely understood and used by stockmen and seedmen in the region. Seed in the Great Plains may be taken 200 to 400 miles north of the area where it was produced without danger of severe winterkilling. Greater northern movement may result in death losses.

Nitrogen is next in importance to water as a limiting factor for plant growth in the West. The two methods which are available for supplying this element are growing legumes or application of commercial fertilizers. Neither potential has been investigated widely on western grasslands. In general, legume plantings have proved more successful than commercial fertilizers. Ensminger *et al.* (1944), working in eastern Washington on an area having about 20 in. annual rainfall, found that smooth brome and crested wheat produced nearly three times as much forage and beef per acre when grown in association with alfalfa as when grown in pure stands. The alfalfa also prevented a sod-bound condition from developing. Barnes and Nelson (1950), working near Cheyenne, Wyoming, found that crested wheatgrass with alfalfa carried about one-third more sheep and produced 50 per cent more lamb gain per acre than did crested wheatgrass alone.

Workers in Australia have found commercial fertilizers to be a necessity for establishment and production of grass-legume pastures. J. G. Davies of Australia reported informally that fertilizer investigations were paramount to the ordinary establishment techniques. He made a simplified statement for emphasis that without fertilizers success was impossible, whereas with proper fertilization failure was impossible.

Most workers in western United States have made a few preliminary trials with fertilizers on new and old stands of grass, mostly with disappointing results. McIlvain and Savage (1950) found that application of ammonium nitrate to weeping lovegrass at 30 pounds of nitrogen in 1947 and 53 pounds in 1948 increased the grazing capacity 33 per cent, gain per head of yearling Hereford steers 9 pounds, and gain per acre 37 pounds. Anderson *et al.* (1946) found that seed and forage yield of smooth brome in Kansas increased with greater amounts of nitrogen up to approximately 100 pounds of that element per acre, and similar results were obtained by Harlan and Kneebone (1953) working with switchgrass. Phosphorus deficiency is so intense on much of the King Ranch in southern Texas that healthful cattle production is impossible without supplemental feeding of phosphorus. The ranch corrected this difficulty and increased forage production by applying superphosphate to vast areas of their range land.

Investigators are continually searching for a satisfactory technique for broadcasting grass seed, either on prepared or unprepared seedbeds, usually with disappointing results. A few exceptions have occurred, and new broadcasting principles are being determined each year. Killough (1950) stated that broadcasting is merely a substitute to be utilized under circumstances where soil treatment or seed covering methods are not practical. He found it essential that grass seeds be covered in some way, such as loose ash from a fire, falling leaves, trampling of livestock, wind, water, or snow.

Recently, broadcasting of pelletized seed was acclaimed revolutionary for range land reseeding. National magazines published spectacular articles on the subject, and newspapers gave it much publicity. Unfortunately the method was not adequately tested before it was widely used. Subsequent tests showed that the pelletizing was detrimental.

Bleak and Phillips (1950) reported on an aerial broadcasting study conducted by the United States Forest Service in southeastern Utah at elevations running from 6500 to 8400 ft. where growing conditions for grass were favorable. Seed pellets were made by the process developed by Dr. L. S. Adams. Six species of grass and one legume were used. Unpelleted grass seed air-sown on the same area at the same time produced 15 to 165 times as many seedlings per square foot as pelleted seed. They found that doubling the number of pellets per square foot did not significantly increase stand. Laboratory germination tests showed seed in the pellets was greatly reduced in germination, and considerable mechanical injury occurred. Tisdale and Platt (1951) also found that compression pellets failed to benefit the seed and had none of the advantages attributed to the method.

Plummer and Stewart (1944) found aerial broadcasting of naked seed successful only on a few favorable sites, foremost of which was aspen ranges of the Intermountain Region. Friedrich (1947) found aerial broadcasting of naked seed feasible on burned-over timberland in Montana.

b. Machinery. Grass establishment by broadcasting does not compare in efficiency with the mechanical placement that can be obtained by using a properly constructed grass drill. An excellent machine for reseeding grass was developed in 1938 at the United States Southern Great Plains Field Station, Woodward, Oklahoma, through the cooperative efforts of the Bureau of Plant Industry, Soils, and Agricultural Engineering, and the Soil Conservation Service (Savage *et al.*, 1948). The drill was equipped to distribute grass seed precisely by using cotton-seeding mechanism which provided positive ejection of light, fluffy, or chaffy seeds; the small seed boxes were equipped with revolving brushes and a base plate with various size holes for fine seeds. An efficient, grain-drill transmission was placed on the machine to obtain the desired rates of seeding. Small, fine seeds could be uniformly sown at rates around ½ pound per acre, whereas light, fluffy seeds could be sown up to 20 pounds per acre. Double-coulter openers equipped with depth flanges were used to prevent the seed from being sown too deeply in soft soils and yet enable sufficient pressure to be put on the openers to cut through stubble-mulch or trash. They found best results were obtained by using press wheels to firmly pack the soil to insure good contact between the seed and soil.

Anderson and Swanson (1949) developed an eccentric disk with a cultipacker seeder attached behind for seeding arid southwestern ranges. Advantages of the machine include commercial availability, rugged construction, ease of use, rapid operation, economy, and lack of need to stay on the contour. Cost of operating this machine was estimated to be $1.50 per acre, exclusive of seed. The machine reduces competition of both perennial and annual plants, and seed is distributed over the entire disturbed area so as to take advantage of varying moisture conditions in the bottom, top, and sides of the pits made by the disk. The United States Forest Service developed an effective brushland machine for plowing range land with minimum breakage. This machine combines desirable features of the Australian stump-jump plow and the wheatland plow (Hull *et al.*, 1950). The brushland plow is sturdy, durable, and effective. Its outstanding feature is the paired disks, mounted with a pitch on jump-arms, which are controlled by springs so that each pair of disks can rise over rocks and brush independently of the other disks and without strain on the plow. Highly effective control of the sagebrush was reported with plows of this type. Also litter and debris are left on the ground to protect soil and grass seedlings, and plowing may be done over long periods of time at costs ranging from $2.50 to $5.00 per acre.

c. Grasses and Legumes. Several new exotic grasses have appeared on western range land during the last 20 years. Some of them show much promise for increasing forage production over adjacent native range, and other equally desirable strains may be discovered among the several introductions (Harlan, 1951).

Crested wheatgrass is undoubtedly the most widespread exotic grass used for reseeding in the United States. Its range is limited to the northern and central regions and to moderate elevations. It is a cool-season grass which is easily established, and which furnishes an acceptable quantity of high-quality forage, particularly in spring. It becomes coarse and lacking in palatability to livestock during midsummer. Crested wheatgrass was introduced into this country in 1898 and again in 1906 (Sarvis, 1941). First plantings were made at Mandan, North Dakota, in 1916, and the grass gained its popularity from seeds sent over the northern Plains from there. The first commercial seed of crested wheatgrass was offered for sale in 1929. The price per pound has fluctuated from 10 cents or less to 75 cents per pound depending upon availability. A uniform seed market is needed for seed of this and other grasses.

Several other introduced grasses have been used with varying success, including intermediate wheatgrass, *Agropyron intermedium*, slender wheatgrass, *Agropyron trachycaulum*, stiffhair wheatgrass, *Agropyron trichophorum*, tall wheatgrass, *Agropyron elongatum*, and Russian wild-rye, *Elymus junceus*. Each of these grasses had a brief flare of popularity, and some of them have found places of permanent use, but none of them have attained the widespread importance of crested wheatgrass. However, crested wheatgrass does not thrive at low elevations in the southern Great Plains nor at extremely high elevations elsewhere. In the latter locations it has been replaced with smooth brome, *Bromus inermis*, timothy, *Phleum pratense*, Kentucky bluegrass, *Popa pratensis*, and varieties of meadow fescue, *Festuca elatior*.

An exotic grass which attained early popularity in the southern United States was Rhodes grass, *Chloris gayana,* which was introduced from South Africa by Cecil Rhodes in 1895. It was easily established and often could be grazed within two months after planting. The grass made two or three seed crops per year, and on fertile soils it yielded up to 6 tons of air-dry forage per acre. Rhodes grass was widely used on the King Ranch in their early days of reseeding. The grass is subject to winterkilling at temperatures of around 16° and 18° F. (Potts and Hensel, 1947). After being cultivated in the United States for nearly 40 years Rhodes grass was beset with a scale insect, *Antonina graminis,* which attained epidemic proportions about 1940; within a few short years wholesale death occurred in many Rhodes grass plantings in the South. The grass is now being replaced in some instances by King Ranch bluestem, Angleton bluestem, *Andropogon nodosus,* blue panicum, *Panicum antidotale,* and buffel grass, *Pennisetum ciliare.*

King Ranch bluestem is believed to have been introduced in the United States about 1905 from China or Eurasia. The grass was rediscovered about 1938 by Nico Diaz of the King Ranch. It had spread from its original small plot for a distance of 7 miles; seed was presumably carried by the prevailing winds.

King Ranch bluestem is easily established, particularly by broadcasting, and is extremely productive, even in relatively low-rainfall areas. It seems to do best on medium-textured soils, but can be grown successfully on both heavy and sandy soils. It is highly alkali tolerant and has been found to thrive on some soils with a white salt crust on the surface. The grass is subject to winterkilling during extremely dry, cold periods. Its northern limit of adaptability seems to be about the 34th degree of latitude in the Plains.

Angleton bluestem, and a closely related species, Kleburg or Diaz bluestem, *Andropogon annulatus,* are similar to King Ranch bluestem except that they require more moisture and are not so cold-hardy. A cold-hardy strain of *Andropogon ischaemum* has been found in Elk County, Kansas, and is being rapidly increased by the Soil Conservation Service at Manhattan, Kansas. Caucasian bluestem is a new Asiatic bluestem which shows promise in Oklahoma, Kansas, and Colorado. It is cold-hardy and is otherwise similar to King Ranch bluestem (Brown, 1953).

Blue panicum was introduced from Australia; it is easily established, it can often be grazed during the first season, and its grazing rate in one test was a cow per acre for a six- or seven-month period (Nixon, 1951). Blue panicum is subject to winterkilling during extremely dry winters. It withstood a temperature of 19° F. below zero at

Woodward, Oklahoma, in 1947 when the soil was moist. However, because of prevalence of dry-freezing, this grass should not be planted north of the 34th degree of latitude.

Buffel grass is an extremely promising grass recently introduced from South Africa. It is a summer-growing, perennial bunch grass primarily adapted to sandy soils. It is subject to winterkilling at about 0° F. It is very productive and palatable.

Weeping lovegrass, Boer lovegrass, *Eragrostis chloromelas,* and Lehman lovegrass, *Eragrostis lehmanniana,* are being widely accepted in arid and semiarid portions of southwestern United States, just as the Asiatic bluestems are being used in the more moist areas. Crider (1945) stated that all three lovegrasses are perennial, come up quickly from seed, grow fast, mature rapidly and early, form deep, dense root systems, set good seed crops, self-seed naturally, are very drought resistant, and are easily destroyed by cultivation when eradication is necessary. They have more seedling vigor, are more easily established, start growth earlier in the spring, recover more rapidly from mowing or grazing, and are more productive than most native and introduced grasses. Lehmann lovegrass is not so productive as weeping or Boer lovegrass. Boer and Lehmann lovegrass are more drought resistant but less cold-hardy than weeping lovegrass.

Staten and Elwell (1944) found weeping lovegrass well adapted and productive on depleted soils in eastern Oklahoma. This vigorous bunch grass can be established on soil so low in fertility that a cover crop cannot be successfully grown. McIlvain and Savage (1950) found weeping lovegrass to have a high carrying capacity but rather low beef-producing value per head; however, beef production per acre was higher than with any other grass tested on the Southern Plains Experimental Range for the six-year period, 1944–1950. Cattle do not relish the grass, but it will produce salable livestock without special treatment. A program of spring fertilization and removal of a hay crop each time the grass grows ahead of the cattle appears to be a promising form of management.

A new discovery on adaptability of a grass was made by Love (1951), working in California with Smilo grass, *Oryzopisis milacea.* Love found this grass to be ideal for reseeding in the ash of brush burns, whereas early establishment trials on well-prepared seedbeds often met with failure. The grass was introduced in the United States in 1879 and received spasmodic attention from time to time, but not until it was tried in the ash of brush burns was its place in revegetation recognized.

Several indigenous species of grass have won acclaim during the last decade. These native grasses were recognized as having potential reseeding value by farsighted range managers.

Sand lovegrass, *Eragrostis trichodes*, is the most notable native grass being used for widespread reseeding in the Great Plains. Seed of this grass was hand-collected near Woodward, Oklahoma, in 1937 under the direction of D. A. Savage. Tests soon confirmed observations that this grass was well adapted to sandy soils in the central and southern Great Plains (Fig. 4). In 1941, seed of this grass was selling for $5.00 a pound, by 1946 the price declined to $2.50, and by 1950 it fell to 25 cents to 35 cents per pound. Owing to lack of harvesting interest and poor seed-producing years in 1951 and 1952, the price per pound rose to $1.00 and $1.25 by January, 1953.

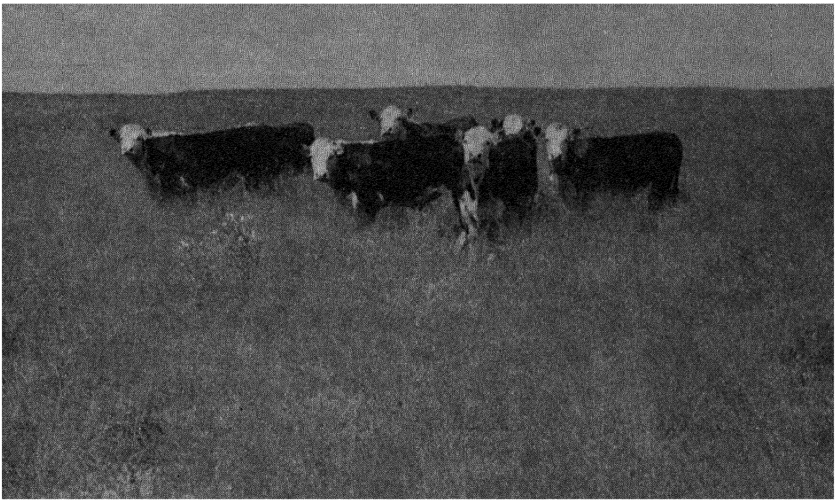

FIG. 4. Yearling steers grazing reseeded sand lovegrass on the Southern Plains Experimental Range near Woodward, Oklahoma. The eight-year average gains from this pasture were 414 pounds per head and 99 pounds per acre as contrasted with only 380 and 41 pounds, respectively, from adjacent, well-managed, native range.

Savage (1947) found that sand lovegrass starts growth early in the spring, produces more total forage, and remains green later in the fall than most native grasses. Stockmen were calling the grass "ice cream grass" because of its high palatability. He also found sand lovegrass equal to the famous shortgrasses, blue grama and buffalo, in average content of protein and minerals. Too, the grass retained about 50 per cent of its nutrients when winter-cured, similar to buffalo and blue grama, whereas most other grasses keep only about 25 per cent of their summer nutrients when dormant. One of the advantages of sand lovegrass is that many of the seeds are hard-coated and do not germinate the first year. Many new seedlings emerge the second year after planting and help to provide a full stand (Brown and McIlvain, 1949a). The grass also reseeds itself well by volunteering.

Legumes are now being investigated for use on western range lands. Love (1952) has found annual clovers to be well adapted to many California range lands. The recommended establishment procedure is to apply 200 pounds of single superphosphate per acre, disk the land, seed a mixture of properly inoculated crimson, rose, and subterranean clover, *Trifolium incarnatum, hirtum,* and *subterraneum,* respectively, at 8 to 10 pounds per acre, and cultipack the area. The cost of this treatment is about $18 to $20 per acre, but the investment is usually more than repaid by increased production the first season.

Sweetclover, *Melilotus sp.,* particularly the yellow-flowered variety, is being used in range land reseeding. The clover is generally seeded at 1 to 2 pounds per acre as a mixture in grass seedings. The plant is biennial but reseeds naturally if given an opportunity through proper grazing management. It responds well to both spring and fall seedings.

A recent new development in the field of dryland forage crops is the advent of drought-resistant, grazing alfalfas, *Medicago sp.* These strains spread and maintain themselves by means of short rootstocks or rhizomes. They are deep-rooted, produce extremely nutritious forage, and are potentially capable of adding fertility to many soils through their symbiotic relationship with nitrogen-fixing bacteria. Aamodt (1952) reported developments during the past 50 years regarding these dry-land grazing alfalfas. Investigations uncovered some startling facts regarding longevity and durability of a few hardy strains. One hardy strain, NOMAD, persisted under 11 in. of rainfall despite annual plowing for 25 years. Aamodt stated that the most promising legume plants for the dry-land West will likely be creeping, drought-resisting alfalfas, especially suited for grazing use.

d. Management. If adapted species are used and become well established, maintenance of the pasture then becomes a simple function of grazing use. However, reseeding usually complicates grazing management procedure. Reseeded areas are much more attractive to livestock than is native range; and much of the total management problem is concerned with separation of the reseeded pastures from native range. Otherwise the principles of management of reseeded pastures are much the same as management of native range; the reseeded plants must be protected from excessive grazing use. As a very rough guide for proper use, between 50 and 75 per cent of the current growth can be removed safely from most reseeded pastures. It is important to keep in mind that management is not so difficult as long as feed supplies are plentiful.

It is generally necessary to fence reseeded pastures separately, and permanent or temporary fences can be used for this purpose. Since establishment of grass usually takes from one to three years under complete protection from grazing, a fence is necessary from the beginning. If the seeded area is much larger in proportion to the native range, it may be satisfactory to leave the areas unfenced and to base carrying capacity largely on the reseeded portion of the range (Passey and Winn, 1953). This practice often results in underuse of the native feed.

Mixtures of grasses complicate management to the extent that many research men are recommending pure stands (Barnes and Nelson, 1950; Stark *et al.*, 1947). However, most natural grasslands consist of mixtures. This fact has prompted many investigators to use mixtures in reseeding work. Advantages of mixtures include superior adaptation to variable soil and seasonal conditions, a better balanced diet for livestock, and more sustained production (McIlvain, 1948).

Mixtures of grasses and legumes are particularly difficult to manage. It has been tentatively determined that most grass-legume mixtures should contain about 50 per cent grass and 50 per cent legume. This proportion provides insurance against bloat from the legume and maintains it as a productive component. Rotation grazing and fertilizing are essential to maintain desirable proportions in a grass-legume mixture. Under some conditions, nitrogen fertilizer can be applied to increase the proportion of grass when the legume percentage gets too high. Similarly, phosphate fertilizers can be applied to promote legume growth when the grass percentage becomes too high.

Pocket gophers in the southern Great Plains pose a problem for the establishment of legumes on dry-land ranges, because legume roots are so palatable. Large-scale control of rodents is not now economically possible; consequently, legume seedings, particularly on sandy soils, may be out of the question until adequate rodent control measures are developed.

e. Grass Breeding. Grass breeding is a relatively new science which offers great possibility for increasing forage production. The science is still in its infancy, and only a few geneticists are engaged in the work. Selection of new grass strains offers quicker results than does development by scientific breeding procedures. However, it is essential that techniques of grass breeding be developed for future use.

The need of the livestock industry is for more total feed. Therefore the primary goal of the grass breeder should be to develop plants capable of producing more total nutrients per acre. A basic concept is involved here, since soil moisture and soil nutrients are limiting factors for forage production. The new plants developed by grass breeders must be able to use the present supplies of moisture and nutrients more efficiently than does the existing vegetation.

Reseeding in the West is hindered greatly because of the difficulty and delay in establishment. Lack of seedling vigor, as explained earlier, is one of the chief difficulties. Grass breeders may be able to overcome this trouble by developing extremely aggressive species. Development of a plant that can be successfully broadcast by airplane into existing vegetation would be an outstanding accomplishment.

Several recent developments have been made in the science of grass breeding. Keller (1944) found that controlled hybridization of some grasses can be effected by distance isolation or by bagging of seedstalks, or by immersion of seed heads in hot water to emasculate female parents. He found smooth brome grass was satisfactorily emasculated by immersion in hot water at 47° or 48° C., for 5 minutes. Several forage grasses, including crested wheatgrass and smooth brome grass, will mature viable seeds on culms detached prior to pollination and placed with cut ends in tap water (Keller, 1943). Harlan (1949) described a strain of side-oats grama, *Bouteloua curtipendula,* which reproduces by producing viable seeds asexually—a process known as apomixis. Progenies of single plant selection are alike in appearance.

Another valuable contribution was made by Keller (1946), who recognized the importance of breeding and selecting plants under competition, as opposed to the much-used system of selecting plants from spaced plantings. He outlined a technique for establishing competitive designs which are subject to statistical analysis.

Love (1951) emphasized the importance of obtaining hybrid vigor in grasses. He stated it may become possible to interplant strains of two species which would cross and produce a population of vigorous hybrids interspersed among the parents. If this goal can be accomplished, the result would be grassland development similar to that of corn hybrids.

New strains of grass resulting from grass breeding include MANDAN wild-rye, NEBRASKA 50 intermediate wheatgrass, REE wheatgrass, LINCOLN, LYON, LANCASTER, AUCHENBACH, FISHER, and MARTIN brome grass, all for use in the northern Great Plains. New species developed in the South include SOUTHLAND brome, MIDLAND Bermuda, TUCSON side-oats grama, EL RENO side-oats grama, BLACKWELL switch grass, and for the Deep South, COASTAL, Bermuda.

IV. CONTROL OF RANGE BRUSH AND WEEDS

Control of range brush and weeds is an effective means of improving production of grazing land. Methods are now available for economical control of many noxious brush species which infest millions of acres of western range land. More economical means are being developed, and it is well within the realm of possibility that complete mastery of most troublesome range plants will occur within the next few years.

1. Scope of Problem

Brush control has not always been a problem associated with western grazing lands. Early range-land history proves that large areas now completely dominated by brush and other undesirable plants were once virgin grasslands. Young *et al.* (1948) quote the personal narrative of a pioneer named Bartlett, who in 1854 described a specific range area in southwest Texas:

> The whole of this district consists of gently undulating plains, without timber save along the margins of the streams, and is covered with the most luxuriant of grass. The indigenous prairie grass is tall, coarse, full of seed at the top, and when young resembles wheat in the spring. But in grasses the glory of the State is the mesquite grass, found only in western Texas. It yields a fine soft sward, preserves its verdue in the winter, and beyond a comparison affords the best wild pasture in the world.

Another early writer, Jared Smith, an employee of the United States Department of Agrostology, wrote in 1898 of the same area previously described by Bartlett. Smith stated that this same region was characterized by a cover of sage and cactus. Today a local resident of the region, J. Frank Dobie, is quoted as describing the area as "chaparral country"; thus, the history of brush invasion is recorded. This same story can be repeated for many areas of the West.

Brush problems of the West consist of 75 million acres of mesquite, *Prosopis juliflora,* in Texas, New Mexico, and Arizona; nearly as much juniper or cedar, *Juniperus sp.,* in the same region; about 115 million acres of big sagebrush primarily along the foothills and lower reaches of the Rocky Mountains, in the Intermountain Region, and in the Great Basin Province; nearly as much "chapparal" (brushland containing several species) on the West Coast, and in Arizona; about 15 million acres of sand sagebrush in the southern Great Plains; and about 12 million acres of shinnery oak, *Quercus havardii,* and over 25 million acres of post and blackjack oak, *Quercus stellata* and *Quercus marilandica,* in Oklahoma and Texas.

a. Detrimental Effects of Brush. Primary effects of brush include serious reduction of forage growth. This is caused by competition for soil moisture, nutrients, and light. Most brush species are deeper rooted than grass and are often better adapted to withstand drought and other inhibiting growth factors (Parker and Martin, 1952). Many brush species also reduce availability of grass to livestock.

Grasses grown in shade of brush are much higher in fiber and much lower in sugar than grasses grown in full sunlight. Hence, they are less nutritious and less attractive to livestock.

One of the most miserable features of dense, tall brush is that it handicaps or prevents handling and caring for livestock. Many valuable range and animal husbandry practices cannot be used on mesquite ranges because the animals cannot be found or herded. Were hoof-and-mouth disease to become present in these areas, the livestock industry would suffer a disastrous loss.

Several of the major brush species are poisonous to livestock and cause much death loss during certain seasons. For instance, 200 breeding cows were killed by shinnery oak poisoning in Ellis County, Oklahoma, in the spring of 1948. The Hoover Ranch near Montoya, New Mexico, figures on an annual loss of 2 per cent of their breeding herd due to cows becoming chronic cactus eaters. The spines cause mouth, stomach, and intestine ulcers which soon result in extreme emaciation and death. These results occurred on a range where the cacti were not thick enough to affect forage production materially.

b. Beneficial Effects of Brush. Many brush species are a source of forage, but often an expensive one. Mesquite beans are often responsible for excellent cattle gains, but since viable seeds are passed through the animals and distributed widely over the range, the value of the feed is questionable. Big sagebrush and sand sagebrush often furnish valuable emergency feed during severe droughts or in winter. For this and other reasons, it may be desirable to control infestations of these two plants without attempting eradication.

Some brush species improve the microclimate and help to enrich the soil. The shade-effect lowers soil and air temperatures. The stature of the brush reduces wind velocity, and leaf transpiration increases humidity. Leaf-drop of deciduous species adds humus to the soil and provides a surface mulch which is effective in erosion control. Many brush species hold snow on areas which would otherwise suffer from lack of snow due to wind removal.

The detrimental effect of brush in reducing availability of forage is counterbalanced to some extent by its enabling protected grasses to produce seed for adjacent areas.

Brush control is an intricate problem. Complexity of the biotic community makes careful study of each species essential in effecting control.

2. *Effects of Brush Control*

Brush control usually increases forage and livestock production, regardless of the climax or nature of the plants The practice makes soil moisture, nutrients, and light immediately available to desirable forage species, which, if they are not present in at least small quantities, must be introduced to the area.

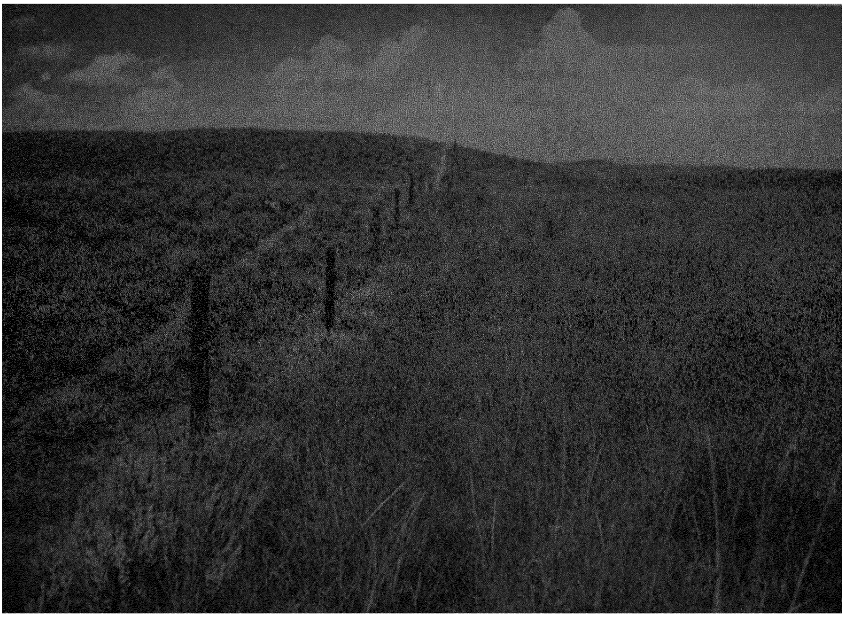

FIG 5 Beneficial effects of sagebrush control on the Southern Plains Experimental Range near Woodward, Oklahoma The pasture on the right was improved by mowing brush and deferring summer grazing in two successive years. Untreated native range is on the left

An important effect of brush control is the fertilizer value of the brush itself For instance, an average stand of sand sagebrush near Woodward, Oklahoma, annually produces about 1500 pounds of air-dry twig and leaf growth per acre. The entire aboveground growth averages about 1.8 tons of air-dry material per acre, whereas the underground portions weigh five times as much In this area brush control provides up to 10.8 tons of organic matter for increased forage production.

Grazing experiments on the Southern Plains Experimental Range show a 70 per cent increase in beef production and net returns from sand sagebrush control (McIlvain and Savage, 1950). Annual production from pastures was 40 pounds of beef per acre compared with 68 on the cleared pastures (Fig. 5). Mesquite control at Spur, Texas, increased beef production 43 per cent during 1948, a very dry year. Brush control in some regions means the difference between no livestock industry and a profitable business enterprise (Love, 1952).

Heavy infestation of weeds also reduce forage production. The competitive nature of western ragweed in Oklahoma is pointed out by Elder (1951). He found that this plant produced 1000 pounds of air-dry foliage per acre in some Oklahoma pastures with subsequent 50 per cent reduction in grass yield.

3. *Recent Developments in Brush Control Methods*

The primary methods of controlling brush are chemical, mechanical, biological, and burning. The most promising method for much rangeland is the use of selective chemicals which kill the brush without seriously injuring desirable forage species. Discovery of 2,4–D, 2,4,5–T, and similar herbicides has made chemical control more feasible. Mechanical control methods depend on bodily removal, injury to the extent the plant succumbs, or repeated removal of aboveground portions to exhaust food reserves in the roots. Many new machines and ingenious principles of use have been devised during the past few years for this purpose. Biological control methods entail either the principle of disease, or destructive use by livestock or insects. Brush control by burning involves the scientific and controlled use of fire either to denude an area or to cause selective killing of undesirable plants.

a. Chemical Control. Hormone chemicals for selective killing of unwanted plants were developed during the latter phases of World War II. At the conclusion of hostilities the chemicals were released for public use. Since that time rapid progress has been made in determining techniques for fast, effective, and low-cost control of unwanted plants. About 27 million pounds of these chemicals are now being used in agriculture each year.

The mechanism by which hormone-type chemicals exert herbicidal effect is not yet clearly understood. It has been deduced that the chemicals bring about a lethal change in plant metabolism. Van Overbeek *et al.* (1951) advanced one of the most reasonable explanations. They stated that high auxin concentrations may cause abnormally high accumulations of metabolites such as coumarin derivatives. One of these derivatives has been shown to be more toxic to broad-leaved plants than to grasses. This may explain both the phytotoxicity and selectivity of 2,4–D and similar herbicides.

Some general statements can be made regarding use of hormone plant killers. With few exceptions, they must be applied when plants are growing actively. They must be applied in a medium which is not greatly injurious to plant cells so that they can be translocated. Surprisingly little chemical is required per acre; lethal dosages for even large woody plants vary between 0:5 and 2 pounds of active ingredient per acre, if refined methods of application are used to secure uniform coverage.

Range land can be successfully sprayed with herbicides, either by airplane or ground equipment. Brown and McIlvain (1949b) listed essentials for efficient application by airplane. These were (1) flight spacing should be no wider than 33 to 45 ft.; (2) an efficient system of flagmen, usually no less than three in number, must be used to guide the pilot; (3) the pilot should fly as close to the ground as possible; (4) spraying should not be done when wind velocity is above 15 miles per hour; (5) spraying should be done cross-wind; (6) the airplane must be properly equipped for uniform distribution, and for positive opening and closing of the valves, and it should have at least two methods of stopping the flow of chemical as a safety precaution; (7) both pressure systems and gravity-flow systems of dispensing chemicals are adequate if properly constructed and used; (8) uniform-sized, medium-coarse droplets are preferable to either fine mists or very large droplets; (9) landing strips should be located within 5 miles of areas to be sprayed; (10) well-equipped tank trucks must be available for efficient loading of the plane; (11) the spray material must be either a solution or a stable emulsion which will hold with mild agitation until it is dispersed; and (12) there is no substitute for experience for pilot, ground crew, and flagmen. Cost of range-land spraying, exclusive of chemicals, is usually about $1.00 per acre—more for extremely small acreages, and less for vast acreages. One spray plane can easily treat 1000 to 1500 acres of range land per day (Fig. 6).

Ground-spraying of range land can be done efficiently with proper equipment. The machines must withstand rough jolting without excessive breakage and without unduly tiring the operator; power wagons, jeeps, or large wheel tractors are best adapted. Brown (1949) described an efficient machine designed for this work. The sprayer was mounted on a four-wheel trailer equipped with springs to ease the terrific jolting. The 20-ft. boom was cross-braced with light weight but rigid conduit pipe to prevent whipping and breakage. A cross-mix mechanical agitator kept the spray material homogeneous. Spraying pressure was maintained by compressed air, eliminating much of the mechanical trouble that occurs with pressure pumps. Line strainers as well as nozzle strainers were provided to prevent nozzle stoppage. A large pressure gauge was mounted where it could be easily seen by the operator.

One of the biggest obstacles to ground spraying is the marking of sprayed swaths. Although flagmen are efficient in airplane spraying, the slow rate of travel of ground machines makes their employment too expensive. Several devices have been tried for automatic marking, but most have been unsatisfactory. A fairly efficient system which is being widely used in the southern Great Plains is a flagman on horseback who precedes the spraying machine. The horse walks in the last wheel track and a light pole, such as a cane fishing rod with a flag on the end, is held to delimit the next swath. The horseman and machine operator usually relieve each other occasionally. Ground machines can usually spray 60 to 100 acres per day at a cost, less chemicals, of about $1.00 to $1.50 per acre.

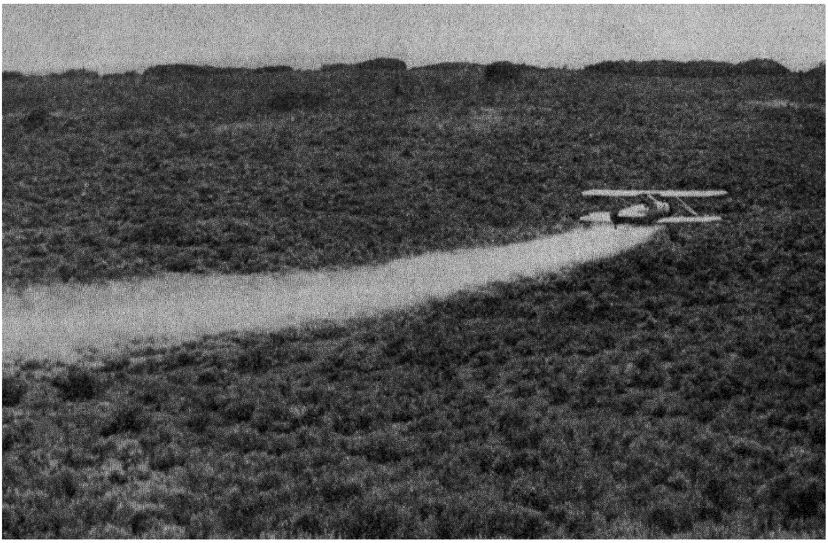

FIG. 6. Spraying sand sagebrush near Woodward, Oklahoma, to increase forage and beef production. Application of 1 pound of 2,4–D in 3 gallons of diesel fuel oil per acre in May at a total cost of about $2.50 per acre usually kills 75 per cent of the brush.

Fisher and Young (1951) developed effective procedures for control of mesquite. Best control resulted from spraying the plants in spring when they reached first heavy foliage stage. Most effective material was ⅔ pound of acid of a low volatile ester of 2,4,5–T in 1 gallon of diesel fuel and 3 gallons of water per acre.

A successful procedure for controlling sand sagebrush is to spray from about May 10 to June 10 with 1 pound acid equivalent of 2,4–D ester in either 3 gallons of diesel oil or 1 gallon diesel oil emulsified with 2 to 4 gallons of water per acre (McIlvain and Savage, 1949). They found that sand sagebrush must be growing actively at the time it is sprayed. If drought prevents rapid growth, it is necessary to defer spraying until the following year.

Seventy to ninety per cent control of big sagebrush was obtained by spraying in early June with 1 to 1½ pounds of 2,4–D per acre (Hervey, 1947; Hull, 1950). Since big sagebrush grows under widely varying conditions, techniques have not been fully developed for adequate control throughout its growth range.

Prickly pear cactus, *Opuntia sp.*, was controlled by use of 2,4,5–T at Woodward. The method was also studied in Texas and published by Young *et al.* (1950). An effective procedure consisted of spraying during the growing season with 0.5 per cent 2,4,5–T in kerosene or diesel oil. The same material gave excellent control of cholla cactus, *Opuntia imbricata*, and blue brush, *Condalia obtusifolia*, at all seasons. Post oak and blackjack oak can be effectively controlled with a hand-applied basal spray of about 0.7 per cent 2,4,5–T in oil during spring.

Elder (1951) eradicated ragweed by spraying it with ¾ pound acid equivalent of 2,4–D ester per acre in spring when plants were 4 to 6 in. high and growing rapidly. He was also able to kill ragweed in lespedeza with this same treatment without severe injury to the legume.

Crabgrass, *Digitaria sanguinalis*, foxtail, *Setaria sp.*, and cheatgrass, *Bromus tectorum*, were successfully controlled by pre-emergence sprays of about 10 pounds of TCA (trichloracetate) per acre (McCall and Zahnley, 1949). These authors found that shallow-rooted grasses were controlled most successfully by applying TCA to the soil after removal of the top growth, whereas grasses with deep root systems were controlled more successfully by foliage applications. Elder (1949) found that Bermuda grass and Johnson grass, *Sorghum halepense*, were controlled by applying about 1 pound of TCA in 1 gallon of water per square rod during midsummer if soil moisture were available. Best results were obtained when TCA was applied on a moist soil followed by scanty rainfall.

b. Mechanical Control. Mechanical control methods are usually more expensive, much slower, and less effective than chemical methods. Costs per acre usually range from $3.00 to $20.00 for a single operation, and retreatment is often necessary. The machinery must be rugged, heavy, and powerful. Even with excellent equipment, mechanical failure is frequent.

Some of the first mechanical brush control work was on sagebrush, using heavy rails to drag the brush. This system was effective only on a few brittle species like big sagebrush which did not resprout. Light plowing with a one-way plow was also tried widely in early days, but was ineffective in most areas. Grubbing by hand or by large machines equipped with dozers, "stingers," crushers, or root plows was usually effective, but the expense was great. However, some of these machines are being widely used today on plants not susceptible to other means of control.

Hollembeak and Muir (1951) reported successful brush control in Monterey County, California, by uprooting "chaparral" in early winter. They pointed out that most of the operation and expense of growing a cultivated crop is for controlling weed competition. Brush is one of the chief competitors of grass, and it is equally as important to reduce this competition as it is to remove weed competition from cultivated crops.

An effective procedure for controlling sand sagebrush by mechanical means was reported by Savage and Costello (1948). Mowing sagebrush in two successive years during June, the time when the roots contain the least quantity of carbohydrates and other foods, was most effective. The sagebrush could be cut with an ordinary heavy duty tractor mower, equipped with sturdy guards and sickle sections. However, breakage with this machinery was quite high and other implements were developed to remove top growth of sand sagebrush. Brush beaters, rapidly revolving axles with chains attached, were designed to shred the brush. They were more effective than the mowers, but were soon replaced by special brush cutters. These are of two main types, one having a single, rapidly revolving cylinder with sharp projections which cuts the brush, and the other a rapidly revolving horizontal blade similar to whirlwind lawn mowers. These machines operate with little breakage and are being widely used to cut sagebrush, skunkbush, *Rhus trilobata,* and sand plum, *Prunus angustifolia,* in the southern Great Plains.

Elwell and Cox (1949) have cut post oak and blackjack oak in Oklahoma with tractor saws, small portable saws, chain saws, tree shears, and rolling cutters. Control, rather than eradication, usually resulted, and retreatment was often necessary. They report forage production increased three to five times after brush control.

An ingenious system of "cabling" mesquite, cedar, and other large brush and trees has been used on thousands of acres in Texas. The method consists of pulling a large cable or anchor chain in a huge "U" with big crawler-type tractors, such as the Caterpillar D-8, pulling on the ends of the cable. The machines travel about 100 ft. apart and can travel from 2 to 5 miles per hour. This method is effective when trees or brush are large enough so that they pull out of the ground rather than bend over.

A notable development in brush control machinery is the brushland plow, which is being used primarily on big sagebrush, as explained in Section III, 2.b. Reseeding is usually necessary after this machine has been used.

c. Biological Control. Biological control of brush is extremely effective when it can be accomplished. Unfortunately there are few biological agencies which cause complete eradication of a particular species without seriously injurying associated vegetation. Goats and sheep have been used to kill some species of brush, and insects have been used to eradicate cactus.

Goats have been used in Texas for many years to kill oak and other brush. In such cases the ranges were divided into small pastures that could be heavily overgrazed, at an intensity of about three goats per acre, until the browse sprouts were completely consumed, after which the goats were moved to another area. This treatment was rather hard on the goats, but sometimes resulted in economically eradicating brush without irreparable damage to other forage plants.

The Cactoblastis insect was transferred without its parasites from the United States to Australia, where it was used effectively in control of cactus on that continent. Some of the insects have been returned to the United States recently in the hopes that a new strain had been produced in Australia that would be resistant to indigenous parasites and could be used here for cactus control.

d. Brush Control by Burning. Fire has long been recognized as an effective tool for destroying troublesome vegetation. Some ecologists are of the opinion that fire is responsible for maintenance of many grassland communities and that lack of fire is responsible for much of the present-day brush invasion of western range lands. Whether this be true or not, it remains a fact that controlled fires are now being used successfully to eradicate several kinds of brush.

Well-planned programs of brush burning can change certain California brushlands into valuable grasslands that produce greater crops of meat and wool (Love and Jones, 1947). A range in Orange County, California, was so heavily infested with brush that cattle would not go through it to harvest the scanty feed supplies. The brush was burned in the fall of 1942, and recovery of bunch grass was almost immediate, reaching a height of 3 ft, on much of the range. There was no evidence of soil erosion after the burn and the 1000 acres carried 300 cattle for seven months of the year. Ash of heavy brush burns was found to be an ideal medium in which to plant seed, but that from grass burns was useless as a seedbed. See Section II, 6 for further information on burning.

V. RANGE NUTRITION AND SUPPLEMENTAL FEEDING

Another major means of increasing range livestock production is through supplemental feeding. The most common form of supplementation, feeding hay, was used by graziers in Biblical times. It is now recognized that various components of a feed may be entirely satisfactory whereas others are lacking, and the wise livestock operator supplements only that portion of the feed which is below par.

1. *Basic Problems*

The problem of determining which nutrients are lacking on a given range for a certain class of livestock is extremely complex. There is great variation in kind of feed consumed by various classes of range livestock and in nutritive content of the vast number of forage species.

Plant scientists have analyzed many species of forage plants to ascertain their nutritive value. Unfortunately much of this work had limited value when applied to livestock usage and needs, because the samples collected for analysis did not represent the feed consumed by livestock, neither as to proportion of each species eaten nor as to selected parts of each plant.

Although scientific skill in the laboratory has been developed to a high degree, standard chemical analyses, as usually run, do not indicate the livestock-producing ability of a forage species. For instance, Savage and Heller (1947) collected and analyzed many samples of sand lovegrass and weeping lovegrass from similar soils and on the same dates. Crude analyses of chemical constituents were nearly the same on the two species of grass. Weeping lovegrass contained slightly more protein, whereas sand lovegrass contained a little more phosphorus. The crude fiber content was nearly the same in both grasses. Despite these similarities, experimental cattle on sand lovegrass gained 115 pounds more per head annually during a six-year grazing study than did cattle on weeping lovegrass. This difference in gain was thought to be due to difference in mechanical breaking strength or digestibility of the two grasses, weeping lovegrass being much the tougher. Nevertheless, the problem remains that laboratory techniques are not always satisfactory for making accurate nutritional determinations of forage species.

The problem is further complicated by numerous variables. Data obtained at Woodward, Oklahoma, show that young grass plants are significantly more nutritious than old plants growing on the same soil type. This confirms findings of other investigators that regrowth on grazed plants is much more nutritious than the green growth of similar, but ungrazed, plants. Savage and Heller (1947) found that most forbs on sandy land in the southern Great Plains contain more phosphorus in summer and less in winter than grasses. Twigs of sagebrush and skunkbrush contained nearly twice as much protein as grasses in late winter. Stoddart and Greaves (1942) determined that grasses were always low compared to other forage groups in protein, fat, calcium, phosphorus, magnesium, sulfur, and calcium-phosphorus ratio, and grasses were at all seasons higher in fiber.

Environmental factors were found by Cook and Harris (1950) to be more important in governing nutrient content of range plants than was chemical content of the soil. Plants growing in aspen, *Populus tremuloides*, areas had a higher protein, phosphorus, and ash content than those on sagebrush areas. Shade and increased soil moisture were thought to be responsible.

An excellent technique for circumventing many of these variables, when comparing one species with another, has been used by Fraps and Fudge (1940). They analyzed over a thousand forage samples from different sites collected at different dates throughout east Texas. Each time a clipping was made Bermuda grass was also collected; thus they were able to compare each species with Bermuda grass and make indirect, but fairly valid, comparisons between species.

It has long been known that livestock prefer a variety of diet. For instance, weeping lovegrass ranks among the lowest in palatability preference for cattle, whereas sand lovegrass ranks at the top. However, cattle on pure stands of sand lovegrass on the Southern Plains Experimental Range have been observed with their heads through the fence grazing weeping lovegrass.

Many stockmen have long wondered if this craving for variety is of practical importance. An answer to this question is provided by Costello (1942), who found that consistent differences of 35 to 60 pounds in seasonal gains of yearling Herefords grazed in a series of experimental pastures were not explainable on the basis of grazing intensity, location of forage, or effect of feeding during the winter. Instead the increased gains appeared to be related to the composition of forage as determined by the percentage of certain grasses, weeds, and shrubs. Costello stated that best cattle gains were obtained when secondary species such as western wheatgrass, red three-awn, *Aristida longiseta*, desert salt grass, *Distichlis stricta*, Russian-thistle, *Salsola sp.*, globe mallow, *Sphaeralcea coccinea*, tansy aster, *Aster sp.*, lambsquarter, *Chenopodium sp.*, pepperweed, *Lepidium sp.*, and fourwing saltbush, *Atriplex canescens*, constituted 10 to 20 per cent of the total forage.

The most plausible explanation for differences in selective grazing is that livestock graze each variety when it is most palatable and nutritious. Since these species do not reach this optimum value at the same time, the period of excellent grazing is prolonged when several species are present in a pasture. Further investigations may lead to other explanations.

Although a variety of forage has been shown to be necessary for maximum livestock gains, extreme use of the principle can be detrimental. For instance, Sarvis (1941) found that six steers turned into a luxuriant stand of sweet clover for one month in midseason gained only 42 pounds per head, whereas comparable steers that had been on pasture the entire season gained 76 pounds during the 30-day period.

A simple explanation might be that the cattle did not relish the forage and ate less of it. However, the answer may be that the abrupt change of diet disrupted the rumen flora. There is good reason to support this possibility. Different kinds of vegetation are known to change pH of the rumen, and slight changes in acidity are known to affect greater changes within the rumen. Thus it can be seen that frequent changes of livestock diet may easily influence animals adversely. There is need for additional information in this field of range nutrition.

Harris *et al.* (1952), working in the mountains and desert of central and western Utah, developed equipment and techniques for conducting detailed feeding trials using several supplements, or combinations, to determine effects upon sheep production. They have developed individual portable feeding pens, portable weighing crates, and a portable chemical laboratory.

Reid *et al.* (1952) suggested an unusual method for determining the dry-matter intake of grazing animals as well as the digestibility of the consumed forage. A naturally occurring plant chromogen absorbing light at 406 μ was used as an indicator. Fecal collections provided the samples for analysis. The method is subject to statistical interpretation and is unique in principle. Refinement of this technique, and availability of facilities for using it widely, should enable investigators to solve many problems heretofore considered impossible to investigate.

New concepts of an adequate plane of nutrition and of proper supplementation to attain that level are being developed rapidly. Many new principles apply throughout the western range, whereas others pertain only to local or limited regions.

2. *Range Supplements*

Supplemental feeding can be divided into total energy intake, proteins, minerals, vitamins, and antibiotics. Proper supplementation, that which produces and maintains the most profitable livestock enterprise, depends upon wise choice of both kind and quantity of additional feeds.

a. Total Feed Intake. The greatest nutritional problem which plagues livestock operators throughout the West is that of supplying adequate total feed intake. Gene F. Payne of the Range Management Department of Montana State Agricultural College aptly states that "hollow-belly disease" causes more livestock loss than any other factor in Montana.

If the livestock of old graziers in Biblical days were doing poorly, the solution was, if possible, to provide a greater quantity of feed. The same remedy holds today. More feed can be provided each animal only by growing cultivated feed crops, by allowing more acreage for grazing, by making two blades of grass grow where only one grew before, by making a long blade of grass replace a short blade, or by increasing digestibility.

Temporary pastures are being used to supplement native range and increase total feed intake. Fall and spring grazing on winter wheat in the Great Plains is a common practice. Oats, barley, and rye are planted for grazing in various other regions of the West (Hollembeak and Muir, 1951). A packing rain is usually necessary before the start of fall grazing. Clay soils are usually more safely grazed than sandy soils. All grazing must be discontinued in the spring at the start of rapid flush of growth if grain is to be produced. Some investigators have shown an advantage of 1 to 2 bushels per acre following grazing, primarily because of increased stooling. Grazing also helps reduce the volume of top growth, with the result that plants do not use so much soil moisture.

Feed crops such as Sudan grass, *Sorghum vulgare* var. *sudanese*, or other forage sorghums are being used to supplement native range in the southern Great Plains. An operator near Canadian, Texas, has a ranch consisting of 7000 acres of native range and 700 acres of cultivated land. Livestock are his only produce. He plants the 700 acres to forage sorghums and makes silage for use as winter feed. The aftermath growth of the sorghum makes excellent fall and early winter pasturage.

This operator states that 700 acres of cultivated land can support his entire herd during the winter; therefore he has been able to increase his ranch stocking capacity one-third. This practice is becoming more widely used every year and is an excellent means of supplementing range feed.

b. Proteins. Next to total feed intake, protein is the limiting factor for good livestock gains. An 8 per cent protein content of range forage is usually adequate. Unfortunately, this condition exists for only three to six months while the grasses are green; and livestock often graze forage containing less-than-adequate protein for six to nine months. Protein supplements are being widely used to correct this deficiency. These supplements are less bulky and usually much less costly on an animal basis than are the roughages required to increase total feed intake.

Eighty to ninety per cent of the range nutritional deficiencies occur through a combined lack of total feed intake and protein. Owing to the "publicizing" of the importance of minerals, vitamins, and antibiotics by farm magazines and commercial feed companies, many livestock producers make certain their livestock are adequately supplied not with total feed and protein, but with minor supplements which are often unnecessary or of little value.

The most common protein supplement in use today is a pellet made of the meal of cottonseed, soybean, linseed, or peanuts. These plant proteins have approximately the same feed value for ruminants. They usually contain from 36 to 43 per cent protein and are generally fed at the daily rate of 1 to 2 pounds per head to cattle. Alfalfa hay is another good source of protein. Nelson *et al.* (1952a) determined from feeding trials in Oklahoma that approximately 8 pounds of alfalfa hay replaced 2½ pounds of 41 per cent protein cottonseed cake as a winter supplement for commercial cows grazing dry native grass.

Recent developments in the oil processing industry have resulted in removal of much fat from the various meals. Tests reveal that this has not affected the value of the protein as a livestock feed (McIlvain and Savage, 1950). However, a word of caution is in order regarding the solvent extraction of fat from protein meals. Several livestock deaths were reported due to feeding of the new-type meal. The cause of the trouble was determined to be a lethal petroleum solvent used to extract the fat. This trouble has been corrected within the last few months and so far as the authors know, is no longer a threat.

c. Minerals. Numerous studies conducted throughout the West have found phosphorus to be the mineral which most often limits livestock production. Calcium has been found adequate on all western ranges, or if it is limiting, phosphorus is also lacking, and nearly all phosphorus supplements are excellent sources of calcium. None of the trace minerals, copper, cobalt, iron, iodine, manganese, magnesium, zinc, boron, or sulfur have been found to be of economic importance on most western ranges (Nelson *et al.*, 1952b).

Phosphorus deficiency results in a greatly reduced rate of growth in all livestock and in low breeding rates. Symptoms of range phosphorus deficiencies include stiffness in the forequarters, slightly arched back, emaciation, and chewing of miscellaneous material such as wood and bones. Black *et al.* (1943) stated that feeding a phosphorus supplement to cows in tests conducted on the King Ranch in southern Texas increased percentage calf crop from 64 to 85 per cent and increased the weaning weight of calves 69 pounds. Trace minerals did not have any effect upon cattle in this study.

Knox and Watkins (1942) reported on a six-year study of phosphorus feeding in southern New Mexico. They found that a mixture of 50 per cent salt and 50 per cent steamed bonemeal increased percentage calf crop from 81 to 90 per cent and increased the weight of calves from 408 to 442 pounds. These advantages were obtained at a cost of about 60 cents per cow. These authors also stated that 20 pounds of salt is considered an ample annual allowance for range cattle, and annual consumption of more than 30 pounds of salt would appear to be excessive and may indicate a desire for something lacking in the ration.

A word of caution concerning steamed bonemeal is in order. Several outbreaks of anthrax occurred in the cattle industry in 1952. These were reportedly traced to shipments of foreign bonemeal which had not been properly processed after reaching this country. High sustained temperatures are necessary during the steaming process to sterilize the bonemeal. The large reputable feed firms have constantly produced a dependable product.

d. Vitamins. Ruminants require most of the essential vitamins for bodily health. Fortunately, however, they are able to synthesize many of these vitamins within their body if supplied with normally good pasturage. Spielman (1946), among others, reports the synthesis of thiamin, niacin, pyridoxine, riboflavin, pantothenic acid, and vitamin K in the rumen, and ascorbic acid in the body of mature cows. It is necessary, however, to supply a source of vitamin A, D, and possibly E.

Vitamin A appears to be the only vitamin of great concern to the range cattle producer, since sunshine ensures the supply of vitamin D. However, dairymen and purebred breeders need to be concerned with other essential vitamins. Symptoms of vitamin A deficiency include watery eyes, night blindness, birth of weak or dead calves with or without eye lesions, retention of the placenta, severe diarrhea in weak, newborn calves, bodily swelling particularly around the legs, and in severe cases, day blindness, loss of appetite, emaciation, and death (Hart and Guilbert, 1933; Jones *et al.*, 1943; Huffman, 1945).

Vitamin A deficiency occurs only when cattle have been without green feed for long periods, such as a severe summer drought combined with a prolonged winter. Such conditions were described by Hart and Guilbert (1933) in a commercial herd in California. Watkins *et al.* (1950), working in southern New Mexico on desert range which should produce vitamin A deficiencies, have been unable to demonstrate value of vitamin A supplements even in drought years. They stated that vitamin A deficiency might occur only in case of prolonged drought or extremely abnormal conditions which would probably necessitate removal of all cattle from the range. This desert range normally produced a few green plants even in the dry fall, winter, and spring seasons. Moreover, in this area parts of the stems of black grama, *Bouteloua eripoda*, remain green for extended periods when other forage is dry.

Dehydrated alfalfa pellets are commonly used for supplying vitamin A to range livestock. A daily ration of from ¼ to ½ pound provides more than the minimum requirements of vitamin A, as well as being an excellent source of both protein and minerals. Because of the popularity of the subject of vitamin feeding, it is highly probable that some livestock operators are using these pellets to excess, as far as economics is concerned. Pellets are not a cheap source of either protein or minerals and should be fed only when there is an indicated need for vitamin A, usually after three to six months of range feeding on completely dry range. A little greenness of any kind, such as annual grass, annual weeds, or the underbark of palatable shrubs, will provide an adequate quantity of vitamin A.

e. Antibiotics. Antibiotics have not been fully investigated as a source of supplements to ruminants. Antibiotics are used in the pork industry but are generally of no benefit to cattle, presumably because of their adverse action on ruminant microorganisms. Some investigators have had indications that antibiotics may be of some value for prevention of diarrhea in newborn calves.

The feeding of phenothiazine for controlling internal parasites in sheep has become a well-established practice. A few investigators have obtained outstanding results by feeding phenothiazine to cattle. Dr. Brock of the Oklahoma Veterinarian Institute and Dr. Mahew in Louisiana have obtained profitable gains in cattle by daily feeding about 2 to 3 g. of phenothiazine per animal. Further investigations are needed for definite conclusions on this subject.

Investigators have demonstrated that domestic livestock can be vaccinated with an insecticide which causes death to blood-sucking insects. This technique is still in the experimental state, but may be a forerunner of great advancements in the future.

3. New Developments in Supplemental Feeding

New developments in types of supplemental feeds, as well as improved rates and methods of feeding them, are being used profitably by many progressive stockmen. Use of urea as a substitute for part of the plant protein is a promising development. Urea is a white, crystalline, water-soluble, organic compound resembling salt in appearance; it can be converted by ruminal microorganisms into usable proteins. Urea contains about 46 per cent nitrogen, or 287 per cent (46 × 6.25) calculated protein (Jones, 1946). In comparison, a high-protein concentrate such as soybean meal contains about 7 per cent nitrogen or about 44 per cent calculated protein.

Urea can quickly kill livestock if it is fed in excessive amounts. It is useful in building up the nitrogen content of low-protein feed mixtures. It has been satisfactorily and safely fed to cattle as 1 to 2 per cent of the total dry matter of the ration. Pope (1953) stated that pellets containing 50 per cent of their nitrogen as urea, and the remainder as cottonseed meal, were as satisfactory as the natural protein for fattening steers. Urea has no value as a source of crude protein in the ration of hogs, horses, chickens, and turkeys.

A new process for self-feeding protein concentrates is being widely used The method consists of mixing ordinary crushed stock salt with a protein meal such as cottonseed or soybean and giving the livestock free access to the mixture. The salt prevents overuse of the protein. Savage and McIlvain (1952) found that daily consumption of cottonseed meal by weaner steer calves could be maintained at 2 pounds per head by use of about ½ pound of salt for each 2 pounds of meal. Larger cattle required more salt to limit their use of protein, whereas smaller cattle required less Cattle on range supporting a good stand of nutritious feed required less salt to govern consumption than those grazing poor-quality or scanty range. The animals seemed to develop a tolerance for salt as the feeding period progressed, and it was necessary to increase the quantity of salt slightly, about ⅛ pound per head, every two months.

Breeding cows were also fed salt-meal mixtures. About 1 pound of salt was required to limit their daily consumption. This quantity of salt had little or no ill effect under practical range conditions. However, some investigators have reported detrimental results from feeding 1 pound of salt per head per day to lactating cows for long periods such as seven to nine months. They reported that milk supply was greatly diminished and the animals become emaciated.

The Woodward investigations revealed that steers fed salt-meal gain 15 to 20 pounds less per head during winter than similar steers hand-fed cottonseed cake. This gain was not made up in the summer time when the cattle were grazed on grass without supplement. Several factors were probably responsible for this slight decrease. The animals on salt-meal drank slightly more than twice as much water as did other animals. It has been calculated that energy required to warm this additional water to body temperature approximated that required to increase body weight about 15 pounds. The salt-meal fed steers were also observed to make numerous trips between the salt-meal bunk and the nearby water tank, often as many as 12 trips at one feeding period. Unless there is sufficient bunk space for most of the animals to eat at one time, much energy is expended by the animals in feeding. Feeding salt-meal mixtures to steers in late summer at Woodward had no ill effect on gains.

Self-feeding of salt-meal was used on the Jornada Experimental Range in New Mexico to obtain more uniform grazing distribution. The salt-meal bunks were placed ½ to 1 mile away from water, and have drawn cattle to lightly grazed areas without ill effect on the animals. Similar trials at Woodward, Oklahoma, indicated that the quantity of salt required to govern consumption was decreased by placing salt-meal bunks away from water.

Dr. M. C. Franklin, Animal Health Laboratory, Sydney, Australia, informally reported on an interesting study there. Severe droughts frequently plague much of Australia. One such drought recently resulted in the death of over 3 million sheep. It has been a common practice to feed supplements during such periods, but it has not been economically feasible to feed sufficient nutrients to keep all animals alive. Dr. Franklin reported outstanding success in reducing fatalities by feeding these supplements at weekly intervals. All animals obtained their fill, had adequate feed for three to four days, and went completely without feed for the remainder of the week. In his investigations, death losses amounted to less than 10 per cent in the lots fed once weekly. When the same quantity of feed was fed daily, death losses were about 40 per cent. Reported advantage of the weekly feeding was due to the fact that all animals were able to consume their just share of the feed. He emphasized that it was not only the shy and weak feeders which profited by the system but also the naturally slow eaters. It must be remembered that this was survival feeding during drought periods and under different economic standards of livestock raising than are used in the United States. However, the principle is an ingenious one, and it will save livestock producers in Australia millions of dollars annually.

A recent innovation in development of a new feed supply in the United States was reported by Duisberg (1952). An edible livestock feed was prepared from the desert shrub, creosote bush, *Larrea divaricata*, by means of alcohol extraction. Tests showed the feed had nutritional value roughly equivalent to that of alfalfa. It was relatively palatable and could be fed to livestock without amendments. Duisberg stated that although the potential supply of creosote bush in the Southwest is very large, it probably would not be economically practical to harvest it for feed alone. However, there are promising possibilities of developing an industry to utilize associated resins and acids, as well as the feed constituents.

VI. Other Principles of Range Improvement

Other means of range improvement include range tillage, water spreading, poison plant control, rodent control, insect control, and management of wildlife. Each of these factors plays an important part on most western range land. They deserve a more complete discussion than is possible in an article of this scope. Several recent developments of significance have occurred in each of the fields of endeavor.

1. Range Tillage and Water Spreading

Range tillage has been successfully used to increase forage production. Several principles are involved. The ground is roughened so it will hold more water, the soil is loosened to increase rate of percolation as well as aeration, and the vegetation is thinned so that the remaining plants can make more vigorous growth. It is thought that tillage operations aid to break up sod-bound conditions.

Barnes (1950), working in mixed prairie vegetation near Cheyenne, Wyoming, found that spacing of cultivated furrows or corrugations should not be greater than 5 ft. Small furrows spaced about 2 ft. apart were most effective. He found that an eccentric disk, similar to that explained in Section III, 2.b., was the most efficient machine for range tillage. The composition of the vegetation determined success of tillage more than did soil type. Where there was no western wheatgrass or other cool-season species present in the vegetation, the tillage had little beneficial effect. Most of the improvement resulted from increase of rhizomatous midgrasses rather than stimulation of short-grass vegetation. Early spring tillage was most beneficial, although both fall and winter tillage was satisfactory, and it made little difference whether the soil was wet or dry. Reseeding was not generally successful following the tillage operations because of competition from perennial plants present on the land. Mechanical treatment increased carrying capacity for sheep 32 per cent and increased lamb gain 10 pounds per head. Also more perennial grass was left on the pitted pastures at the end of each summer grazing season to hold winter snows.

Water spreading is the technique of using small retention dams, dykes, or furrows for spilling flood waters onto relatively flat and productive lands adjacent to water channels. This procedure has been successfully used to make hay meadows from near-desert land. Complicated systems of terraces have been constructed to zigzag water back and forth across an area so that several acres can be flooded from one diversion dam. Flood waters in some areas carry heavy loads of silt, and it has been necessary in these areas to construct settling ponds to deposit the silt before using the water. Spreader dams, spreader terraces, diversion dams, floodways, baffle dykes, and contour furrows were installed in Logan Gulch, a minor tributary of Wind River in Wyoming, for demonstration and experimental purposes. Benefits of the practice include retention of much silt, reduction of downstream flood damage, regulation of stream flow, and most important—retardation of range deterioration.

An extensive test was made of water-retention and water-spreading structures in semidesert range land in southern New Mexico (Valentine, 1947b). Five types of structures were studied. These consisted of widely spread terraces, small diversion dams, contour channels, brush dams, and various smaller, closely spaced, contoured, earthen structures. None of these installations were found effective for improving vegetative cover, and existing soil factors were thought to be responsible for their failure. Valentine recommended that pilot work on an exploratory scale precede extensive work in any region.

2. *Poison Plant Control*

Poison plant losses have harassed the livestock industry since its inception. The trouble is particularly insidious because numerous losses occur before the cause is recognized. Ill health resulting from consumption of poison plants causes much more economic loss than does death.

One of the earliest cases of recognized plant poisoning occurred in the early days of settlement of this country. So many cattle were killed that a contagious disease was suspected. It appeared to be an epidemic, and the condition was called "milk sickness." It was determined that the trouble could be transmitted from the milk of cows to other animals, including man. The cause was finally established to be white snakeroot, *Eupatorium urticaefolium*, in the eastern part of the United States, and a similar condition was caused by rayless goldenrod, *Aplopappus heterophyllus*, in the West (Marsh, 1929).

The conditions under which most poison plants are eaten include lack of total forage, improperly balanced diet where some nutrients are deficient, disturbed areas, newly plowed areas which occasionally contain poisonous roots, dry or partially dry water holes, curiosity, and occasionally accident (West and Emmel, 1950). Most trouble from poison plants occurs when hungry animals are turned onto a new range for the first time. These animals will be poisoned and die when animals that are indigenous to the area suffer no ill effects.

Probably more livestock losses result from poisoning by common plants such as larkspur, *Delphinium sp.*, Johnson grass, loco weed, *Oxytripis sp.*, and cocklebur, *Xanthium sp.*, than by all of the more notorious species combined. Johnson grass poisoning is caused by prussic acid which is formed by enzymes within the animals. Many other plants including sorghums, particularly sorgos, occasionally develop the same poison. All of these plants should be grazed with caution because poisoning is possible at any time during the growing season. Hay has also been known to carry the poison. Animals should always be well fed before being turned into a field containing these plants.

Cockleburs are poisonous only during the very young stage of development when the first two leaves or cotyledons are present. Management systems devised to avoid grazing of cocklebur-infested areas in early spring are the best means of prevention.

Sweetclover is another commonly grown plant which causes considerable loss in some seasons. The chemical, coumarin, is the poisonous principle. This chemical prevents the clotting of blood, and animals die from wounds, dehorning, castrating, or from internal hemorrhage.

Some weeds are harmful because of their mechanical characteristics. Prickly pear and cholla cactus are examples of these offenders, as explained in Section IV, 1.a. Other plants such as horsetail, *Equisetum sp.*, cause trouble because of a high silica content which acts as an abrasive in the intestinal tract.

An annual poison plant which has received most publicity within recent years is halogeton, *Halogeton glomeratus*, a native of Russia. According to Stoddart *et al.* (1949), it was first found growing in this country in 1935 near Elko, Nevada. It has spread rapidly since. In the fall of 1945, over 750 sheep from one band were killed in one night by halogeton. In 1946, the plant was discovered in eastern California, by 1951 it had made its way to the San Francisco Bay area, and it was found in Colorado in 1953. Halogeton resembles Russian-thistle except at seed stage. Its poisonous property is an oxalate. The plant grows best on bare and undisturbed soil where annual precipitation is from 4 to 15 in., thriving where a native plant cover is thin or low in vigor. It produces an abundance of seed over a long season even on poor soils during dry weather. The seed is capable of germinating nearly 100 per cent within a few days after it has matured on the plant (Anonymous, 1951).

Although 2,4–D is effective in killing halogeton when used at the rate of 2 pounds acid equivalent per acre in midsummer, the most economical and effective control is good range management. The plant cannot invade good-condition range, and restoration of good perennial species quickly crowds it out (Erickson, 1951).

3. *Rodent Control*

Rodents are often responsible for destruction of much range forage. Their effect has been found particularly detrimental during drought periods. Not only do they compete directly with livestock for forage, they cut, injure, or destroy many plants in their burrowing activities. They create a further menace by distributing seed of noxious plant species (Reynolds and Glendening, 1949). However, all effects of rodents are not injurious. They often aid range land by distributing and planting seed of desirable species. Their burrowing tends to loosen soil compacted by grazing animals, *i.e.*, they effect a natural form of tillage. Their activities are no doubt part of the complex which maintains the various vegetative types.

Prairie dogs were early recognized as destructive users of the range. Their living habits made control with strychnine-treated grain a simple matter. During the early days of the Works Progress Administration, prairie dogs on millions of acres were poisoned by federal agencies. Progressive stockmen also helped wage this war, and the prairie dog was controlled to the point that he was no longer considered a serious range pest. Stockmen have taken little note of his activity during the last decade, with the result that dog numbers have increased greatly in some areas. The Indian Service of the United States Department of the Interior treated 42,000 acres in South Dakota in 1951.

Preliminary data obtained on the Southern Plains Experimental Range near Woodward, Oklahoma, indicate the loss caused by rodents in some areas. W. J. Frank, working with the Oklahoma Cooperative

Wildlife Unit, determined that about 30 pounds live-weight of rodents were annually produced per acre on sandsage grasslands. This production included all types of rodents, including pocket gophers, kangaroo rats, pack rats, ground squirrels, cotton mice, grasshopper mice, cottontail rabbits, and jack rabbits. The importance of this figure is emphasized when compared with 39 pounds per acre of annual beef production on the same range.

The food habits of pocket gophers are thought to be largely responsible for the absence of fleshy-rooted forbs and desirable legumes in the Southern Great Plains. Specific instances occur where entire colonies of legumes have been eradicated during a single winter by heavy infestations of pocket gophers.

Moore and Reid (1951) reported results of a 17-year study on the effect of pocket gophers in the Blue Mountains of eastern Oregon. They determined that gophers feed mainly on surface vegetation in the vicinity of their runways, on fleshy roots, and on underground stems. The average daily consumption per gopher was 71 g. green feed. Pocket gophers clearly had an adverse effect on poor condition ranges in that they increased low-value annual weeds.

Norris (1950) reported on an eight-year study of rodents, rabbits, and cattle on two vegetative types on semidesert range land. Rodent control resulted in excellent improvement of valuable grass in the mesquite-snakeweed type, but no appreciable benefits resulted from control in good black grama grassland. Forage production was increased about fivefold by excluding rodents and rabbits. Norris believes, however, that benefits from rodent control in the mesquite-snakeweed type will not offset control costs.

Rodent control must be conducted on a co-operative basis throughout large areas; otherwise reinvasion of rodents from adjoining areas will soon nullify the effects of treatment (Hoerner, 1945). Precise experimental investigations are necessary to determine relative detrimental and beneficial effects of rodents before control programs are initiated.

4. *Insect Control*

Grasshoppers are one of the most destructive range insects. They are an annual problem in many areas and are recognized as public problems in such areas. They usually consume the greenest, most lush, and most nutritious forage, and they are particularly destructive to young grass seedings. Young stands have been completely destroyed in a few days by relatively light infestations of grasshoppers. Grasshopper control on range land is effected by two general methods, spreading of poison bait and use of insecticidal sprays or dusts. Both methods are effective when properly employed.

The Rhodes grass scale insect had a profound effect on the grasslands of the southern United States. These insects devastated large areas of highly productive Rhodes grass, often leaving not even straggler plants as evidence that Rhodes grass once occupied the area. No practical means were discovered to combat the pest. Fortunately the insects did not turn to other species after they killed the Rhodes grass.

South Texas range land has another insect pest of economic importance, the white ant or grass termite. These termites cause damage by destroying all surface litter; this leaves the soil bare and subject to raindrop compaction, runoff, baking by the sun, and excessive evaporation. The insects also cover much of the living vegetation with particles of earth which destroy its value as forage. There is no known economical means of controlling this insect. Good range management is an aid, since it results in vigorous plant growth.

Another insect which has greatly reduced forage production in some areas is the common red ant. These mound-building insects often denude areas 10 to 15 ft. in diameter. Whole landscapes become pockmarked with the characteristically round bare spots. Both federal and state programs have been instituted for their control. The new insecticides, chlordane and heptachlor, are cheap and effective means for controlling this pest, but like the prairie dog, these insects will reinfest areas after control measures are relaxed, and constant vigilance is required to prevent their destructivity (Knowlton, 1952).

All of the foregoing range pests, *i.e.*, poison plants, rodents, and insects, produce their most destructive effects during drought periods when forage is scarce. However, their detrimental effect is a continuous and insidious one which only becomes more apparent during periods of feed shortage. Constant effort on the part of all grassland users is necessary for effective control.

5. *Wildlife Management*

Big game, primarily deer, elk, and antelope, have become a major problem on many western range lands. Cooney (1952) aptly described one example typical of happenings throughout much of the West. He stated that elk, buffalo, antelope, and deer were abundant on the foothill ranges of the Rocky Mountains at the time of Lewis and Clark. Between 1880 and 1884 the northern herd of buffalo, estimated to number 1 million animals, was almost completely annihilated by hide hunters. Elk faired little better, and by 1900 only a few head could be found deep in the inaccessible mountain ranges. Restoration of elk herds started in 1910 from Yellowstone Park. There are now 40,000 elk in Montana alone, and these animals have become a problem in other important uses of the land. Critical problems usually arise over winter ranges. The game animals forage high in the mountains during summer and usually cause little concern at that time of year. In winter they concentrate in the valleys and often cause untold damage to meadows, haystacks, fruit trees, and ornamental shrubbery.

Utah's big game population consists of approximately 223,000 deer, 5300 elk, and 1900 antelope, equivalent in body weight to 40,600 cattle or 325,000 sheep (Stoddart and Rasmussen, 1945). Throughout Utah winter feed is the big problem.

The big game problem is becoming well appreciated by the public, and progress is being made in correcting conflict between big game and livestock producers. Special and extended hunting seasons are becoming more common, and it is now realized that reduction of female animals as well as male animals is the key to reduction of total numbers. Several state wildlife agencies are purchasing winter range for wildlife. Special fences are being constructed by state and federal agencies to prevent big game from molesting private individuals. Outrigger electric fences, regular fences with electric lines 3 to 4 ft. out, have been found to be satisfactory as barriers for big game. Howard and Hjersman (1951) have recently developed a procedure for spraying fruit trees with deer repellents to prevent deer damage during winter.

Conservation committees are being formed to work out the difficult problems, and range managers are making valuable contributions by learning and publicizing new facts about wildlife habits as well as new principles concerning the dual management of livestock and big game. The solution lies in good range management and maintenance of big game numbers in balance with range forage supplies.

References

Aamodt, O. S. 1952. *What's New in Crops & Soils* **5** (1), 7–10.

Adams, F., Ewing, P. A., and Huberty, M. R. 1947. California Division of Forestry.

Aldous, A. E. 1934. *Kansas Agr. Expt. Sta. Tech. Bull.* **38.**

Anderson, D., and Swanson, A. R. 1949. *J. Range Management* **2,** 64–66.

Anderson, K. L., Krenzin, R. E., and Hide, J. C. 1946. *J. Am. Soc. Agron.* **38,** 1058–1067.

Anonymous. 1951. *Westland Pasture J.* **2,** 1–6.

Barnes, O. K. 1950. *J. Range Management* **3,** 198–203.

Barnes, O. K., Lang, R. L., and Beetle, A. A. 1950. *Wyoming Agr. Expt. Sta. Bull.* **299.**

Barnes, O. K., and Nelson, A. L. 1950. *Wyoming Agr. Expt. Sta. Bull.* **302.**

Bentley, H. L. 1898. *U. S. Dept. Agr. Farmers' Bull.* **72.**

Black, W. H., and Clark, V. I. 1942. *U. S. Dept. Agr. Circ.* **642.**

Black, W. H., Tash, L. H., Jones, J. M., and Kleberg, R. J. 1943. *U. S. Dept. Agr. Tech. Bull.* **856.**

Bleak, A. T., and Phillips, T. A. 1950. *U. S. Dept. Agr. Forest Service Research Paper* **22.**

Borst, H. L., and Woodburn, R. 1942. *U. S. Dept. Agr. Tech. Bull.* **825.**

Bridges, J. O. 1942. *New Mexico Agr. Expt. Sta. Bull.* **291.**

Brown, A. L. 1949. *Agron. J.* **41,** 47–48.

Brown, A. L., and McIlvain, E. H. 1949a. *What's New in Crops & Soils* **1** (9) 14–15.

Brown, A. L., and McIlvain, E. H. 1949b. *Agron. J.* **41,** 96–97.

Brown, H. L. 1953. *Kansas Stockman,* January.

Clarke, S. E., and Heinrichs, D. H. 1941. *Canadian Dept. Agr. Farmers' Bull.* **103.**

Clarke, S. E., Tisdale, E. W., and Skoglund, N. A. 1947. *Can. Dept. Agr. Tech. Bull.* **46.**

Cook, C. W., and Harris, L. E. 1950. *Utah Agr. Expt. Sta. Bull.* **344.**

Cooney, R. F. 1952. *J. Range Management* **5,** 3–7.

Costello, D. F. 1939. *U. S. Dept. Agr. Tech. Bull.* **686.**

Costello, D. F. 1942. *Colorado Farm Bull.* **IV,** 14–15.

Costello, D. F. 1944. *Colorado Agr. Expt. Sta. Bull.* **383-A.**

Costello, D. F., and Schwan, H. E. 1946. U. S. Dept. Agr. Forest Service Unnumbered Processed Rept., April.

Craddock, G. W., and Forsling, C. L. 1938. *U. S. Dept. Agr. Tech. Bull.* **600.**

Crider, F. J. 1945. *U. S. Dept. Agr. Circ.* **730.**

Doran, C. W. 1951. *U. S. Dept. Agr. Forest Service Rocky Mountain Forest & Range Expt. Sta. Paper* **6.**

Duisberg, P. C. 1952. *J. Animal Sci.* **11,** 174–180.

Duley, F. L., and Domingo, C. E. 1949. *Nebraska Agr. Expt. Sta. Research Bull.* **159.**

Dyksterhuis, E. J. 1949. *J. Range Management* **2,** 104–115.

Elder, W. C. 1949. *Farm & Ranch,* June.

Elder, W. C. 1951. *Oklahoma Agr. Expt. Sta. Bull.* **B-369.**

Ellison, W. D. 1944. *Agr. Eng.* **25,** 131.

Ellison, L., Croft, A. R., and Bailey, R. W. 1951. *U. S. Dept. Agr. Handbook* **19.**

Elwell, H. M., and Cox, M. B. 1949. *Oklahoma Agr. Expt. Sta. Progress Rept.* **M181.**

Elwell, H. M., Daniel, H. A., and Fenton, F. A. 1941. *Oklahoma Agr. Expt. Sta. Bull.* **B-247.**

Ensminger, M. E., McDonald, H. G., Law, A. G., Warwick, E. J., Kreizinger, E. J., and Hawk, V. B. 1944. *Washington Agr. Expt. Sta. Bull.* **444.**

Erickson, L. C. 1951. *Idaho Agr. Expt. Sta. Circ.* **117.**

Fisher, C. E., and Young, D. W. 1951. *The Cattleman* **37,** 22–23.

Flory, E. L., and Marshall, C. G. 1942. *U. S. Dept. Agr. Farmers' Bull.* **1913.**

Franzke, C. J., and Hume, A. N. 1942. *South Dakota Agr. Expt. Sta. Bull.* **361.**

Fraps, G. S., and Cory, V. L. 1940. *Texas Agr. Expt. Sta. Bull.* **586.**

Fraps, G. S., and Fudge, J. F. 1940. *Texas Agr. Expt. Sta. Bull.* **582.**

Friedrich, C. A. 1947. *U. S. Dept. Agr. Forest Service Northern Rocky Mountain Forest & Range Expt. Sta., Research Notes* **52.**

Hamilton, C. L., and Jepson, H. G. 1940. *U. S. Dept. Agr. Farmers' Bull.* **1859.**

Harlan, J. R. 1949. *Am. J. Botany* **36,** 495–499.

Harlan, J. R. 1951. *J. Range Management* **4**, 16–18.

Harlan, J. R., and Kneebone, W. R. 1953. *Agron. J.* **45**, 385–386.

Harper, H. J. 1947. *Oklahoma Agr. Expt. Sta. Misc. Publ.* **10.**

Harris, L. E., Cook, C. W., and Stoddart, L. A. 1952. *J. Animal Sci.* **11**, 181–190.

Hart, G. H., and Guilbert, H. R. 1933. *California Agr. Expt. Sta. Bull.* **560.**

Hervey, D. F. 1947. *Colorado A. & M. News* **2**, 7.

Hoerner, J. L. 1945. *Colorado Agr. Ext. Circ.* **121-A.**

Hollembeak, H. D., and Muir, J. 1951. California Agr. Ext. Service Mimeo. Rept.

Holt, E. C., Potts, R. C., and Fudge, J. F. 1951. *Texas Agr. Expt. Sta. Circ.* **129.**

Hopkins, H. 1941. *Trans. Kansas Academy Sci.* **44**, 10 pp.

Hopkins, H., Albertson, F. W., and Reigel, A. 1948. *Trans. Kansas Academy Sci.* **51**, 131–141.

Howard, W. E., and Hjersman, H. A. 1951. *California Agr.* **5**, 7.

Huffman, C. F. 1945. *Nat. Butter Cheese J.* **36**, 90.

Hull, A. C. 1950. U. S. Dept. Agr. Forest Service Rocky Mountain Forest & Range Expt. Sta. unnumbered mimeo. rept.

Hull, A. C. Jr., and Doran, C. W. 1950. *U. S. Dept. Agr. Forest Service Rocky Mountain Forest & Range Expt. Sta. Paper* **4.**

Hull, A. C. Jr., Doran, C. W., Wasser, C. H., and Hervey, D. F. 1950. *Colorado Agr. Expt. Sta. Bull.* **413-A.**

Humphrey, R. R. 1945. *J. Forestry* **43**, 646–647.

Ittner, N. R., and Kelly, C. F. 1951. *J. Animal Sci.* **10**, 184–194.

Jardine, J. T. 1915. *U. S. Dept. Agr. Yearbook*, pp. 299–310.

Jones, I. R. 1946. *Oregon Agr. Expt. Sta. Circ.* **373.**

Jones, J. H., *et al.* 1943. *Texas Agr. Expt. Sta. Bull.* **630.**

Karraker, P. E. 1951. *Kentucky Agr. Expt. Sta. Bull.* **561.**

Keller, W. 1943. *J. Am. Soc. Agron.* **35**, 617–624.

Keller, W. 1944. *J. Heredity* **35**, 49–56.

Keller, W. 1946. *J. Am. Soc. Agron.* **38**, 580–588.

Killough, J. R. 1950. *J. Range Management* **3**, 33–41.

Knowlton, G. F. 1952. *Farm & Home Sci. (Utah Agr. Expt. Sta.)* **13**, 96–97.

Knox, J. H., and Watkins, W. E. 1942. *New Mexico Agr. Expt. Sta. Bull.* **287.**

Love, R. M. 1951. *California Agr.* **5**, 8–10.

Love, R. M. 1952. *Westland Pasture J.* **3**, 1–4.

Love, R. M., and Jones, B. J. 1947. *California Agr. Expt. Sta. Circ.* **371.**

McCall, G. L., and Zahnley, J. W. 1949. *Kansas Agr. Expt. Sta. Circ.* **255.**

McIlvain, E. H. 1948. *Oklahoma Agr. Expt. Sta. Bull.* **B-319.**

McIlvain, E. H., and Savage, D. A. 1949. *J. Range Management* **2**, 43–52.

McIlvain, E. H., and Savage, D. A. 1950. U. S. Dept. Agr. BPISAE Southern Great Plains Field Sta. Mimeo. Rept.

McIlvain, E. H., and Savage, D. A. 1951. *J. Range Management* **4**, 42–47.

Marsh, C. D. 1929. *U. S. Dept. Agr. Farmers' Bull.* **1593.**

Miles, A. D. 1951. *J. Range Management* **4**, 228–232.

Moore, A. W., and Reid, E. H. 1951. *U. S. Dept. Agr. Circ.* **884.**

Mueggler, W. F. 1950. *J. Range Management* **3**, 308–315.

Nelson, A. B., Darlow, A. E., MacVicar, R. W., and Campbell, W. D. 1952a. *Oklahoma Agr. Expt. Sta. Misc. Publ.* **MP-27**, 29–33.

Nelson, A. B., Nance, J. A., Gallup, W. D., and Darlow, A. E. 1952b. *Oklahoma Agr. Expt. Sta. Misc. Publ.* **MP-27**, 9–13.

Nixon, W. M. 1949. *J. Range Management* **2**, 213–217.

Nixon, W. M. 1951. *What's New in Crops & Soils* **4,** 26.
Norris, J. J. 1950. *New Mexico Agr. Expt. Sta. Bull.* **353.**
Osborn, B. 1952. *J. Range Management* **5,** 408–414.
Parker, K. W. 1951. U. S. Forest Service U. S. Dept. Agr. unnumbered Processed Rept.
Parker, K. W., and Martin, S. C. 1952. *U. S. Dept. Agr. Circ.* **908.**
Passey, H. B., and Winn, D. S. 1953. *J. Range Management* **6,** 11–15.
Pearse, C. K., Plummer, A. P., and Savage, D. A. 1948. "Grass." *U. S. Dept. Agr. Yearbook,* pp. 227–233.
Pechanec, J. F. 1944. *U. S. Dept. Agr. Farmers' Bull.* **1948.**
Peterson, M. L. 1951. *Westland Pasture J.* **2,** 5.
Pickford, G. D., and Jackman, E. R. 1944. *Oregon Agr. Expt. Sta. Circ.* **159.**
Plummer, A. P., and Stewart, G. 1944. *U. S. Dept. Agr. Forest Service Intermountain Forest and Range Expt. Sta. Research Papei* **11,** 1–6.
Pope, L. S. 1953. *The Farmer-Stockman,* January, 8.
Potts, R. C., and Hensel, R. L. 1947. *Texas Agr. Expt. Sta. Circ.* **116.**
Reid, J. T., Woolfolk, P. G., Hardison, W. A., Martin, C. M., Brundage, A. L., and Kaufmann, R. W. 1952. *J. Nutrition* **46,** 255–269.
Reynolds, H. G., and Glendening, G. E. 1949. *J. Range Management* **2,** 193–197.
Rhoad, A. O., and Black, W. H. 1943. *U. S. Dept. Agr. Circ.* **673.**
Rogler, G. A. 1951. *J. Range Management* **4,** 35–41.
Sampson, A. W. 1913. *U. S. Dept. Agr. Bull.* **34.**
Sampson, A. W. 1949. *Proceedings of the United Nations Scientific Conference on the Conservation and Utilization of Resources* **VI,** 509–514.
Sarvis, J. T. 1941. *North Dakota Agr. Expt. Sta. Bull.* **308.**
Savage, D. A. 1939. *U. S. Dept. Agr. Circ.* **491.**
Savage, D. A. 1947. *Country Gentleman.*
Savage, D. A., and Costello, D. F. 1948. "Grass." *U. S. Dept. Agr. Yearbook,* pp. 522–537.
Savage, D. A., and Heller, V. G. 1947. *U. S. Dept Agr. Tech. Bull.* **943.**
Savage, D. A., and McIlvain, E. H. 1952. U. S. Dept. Agr. BPISAE Southern Great Plains Field Sta. mimeo. rept.
Savage, D. A., Smith, J. E., and Costello, D. F. 1948. "Grass." *U. S. Dept. Agr. Yearbook,* pp. 506–522.
Shantz, H. L. 1947. California Division of Forestry.
Short, L. R. 1943. *U. S. Dept. Agr. Farmers' Bull.* **1924.**
Spielman, A. A. 1946. *Flour and Feed* **46,** 22.
Stark, R. H., Toevs, J. L., and Hafenrichter, A. L. 1947. *Idaho Agr. Expt. Sta. Circ.* **112.**
Staten, H. W., and Elwell, H. M. 1944. *Oklahoma Agr. Expt. Sta. Bull.* **281.**
Stewart, G. 1950. *J. Range Management* **3,** 52–59.
Stoddart, L. A. 1946. *Utah Agr. Expt. Sta. Circ.* **122.**
Stoddart, L. A., and Greaves, J. E. 1942. *Utah Agr. Expt. Sta. Bull.* **305.**
Stoddart, L. A., Holmgren, A. H., and Cook, C. W. 1949. *Utah State Agr. College Spec. Rept.* **2.**
Stoddart, L. A., and Rasmussen, D. I. 1945. *Utah Agr. Expt. Sta. Circ.* **121.**
Stoddart, L. A., and Smith, A. D. 1943. "Range Management." McGraw-Hill Book Company, New York.
Talbot, M. W. 1937. *U. S. Dept. Agr. Farmers' Bull.* **1782.**
Theron, J. J. 1951. *J. Agr. Sci.* **41,** 289–296.

Tisdale, E. W., and Platt, K. B. 1951. *Univ. of Idaho Special Research Rept., Project* **16.**

Tomanek, G. W. 1948. *Trans. Kansas Academy Sci.* **51,** 171–196.

Turner, G. T., and Klipple, G. E. 1952. *J. Range Management* **5,** 22–28.

Valentine, K. A. 1947a. *J. Forestry* **45,** 749–754.

Valentine, K. A. 1947b. *New Mexico Agr. Expt. Sta. Bull.* **341.**

Van Overbeek, J., Blondeau, R., and Horne, V. 1951. *Plant Physiol.* **26,** 687–696.

Wasser, C. H. 1950. Colorado Agr. Expt. Sta. unnumbered mimeo. circ.

Watkins, W. E., Knox, J. H., and Benner, J. W. 1950. *New Mexico Agr. Expt. Sta. Bull.* **355.**

West, E., and Emmel, M. W. 1950. *Florida Agr. Expt. Sta. Bull.* **468.**

Woolfolk, E. J., and Knapp, B. 1949. *Montana Agr. Expt. Sta. Bull.* **463,** 1–26.

Young, V. A., Anderwald, F. R., and McCully, W. G. 1948. *Texas Agr. Expt. Sta. Misc. Publ.* **21.**

Young, V. A., Fisher, C. E., Darrow, R. A., McCully, W. G., and Young, D. W. 1950. *Texas Agr. Expt. Sta. Bull.* **721.**

Requirement and Availability of Soil Water

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I. INTRODUCTION

This paper will deal with the broad aspects of the subject including water requirement, the consumptive use of water in plant growth, total use of water on the farm, and the availability of water as related to the nature and distribution of plant roots and to moisture stress in the soil.

A knowledge of the amount of water required to produce crops is essential to agriculturists. In the Western United States, and more recently in the Midwest and humid areas, irrigation is being more frequently used either as the major source of water or to supplement natural rainfall. In planning for irrigation it becomes essential to know something about the quantity of water consumed in growing a crop and the efficiency with which water can be applied. Such information is not only necessary in planning for large irrigated projects, but it is also needed in planning individual farm systems or layout and in improving irrigation practices. Although it is important to know how much land can be served by a specific amount of water in the more humid areas, it is imperative to have this information in the arid West in order to obtain most efficient utilization of limited water resources with a minimum construction cost of canals and distribution systems. With the present high cost of construction it is almost as great an error to have too large a distribution system as it is to have too small a system which does not provide adequate water for maximum plant growth. It is important, therefore, for all to know more about the amount of water that is required in a given locality and on given farms by crops in order that maximum production can be obtained.

Unfortunately the terminology used to describe the amount of water required for crop growth is confusing. Briggs and Shantz (1917) define the term "water requirement" as the ratio of the weight of water absorbed by a plant during its total period of growth to the weight of dry matter (exclusive of roots) produced during the same period. Although this is the definition that will be used in this paper, water requirement to many, especially in the irrigated region, frequently has a broader connotation. Many farmers and water users and some scientists working in the field of irrigation have come to refer to water requirement as the amount of water needed for a given field or farm to produce a satisfactory type of growth for their various crops. When used with this latter meaning, the term "water requirement" includes water used by plants in transpiration or production of tissue (Briggs and Shantz water requirements), water lost by evaporation from the soil or plant surfaces, and the water normally lost during irrigations as a result of inefficiencies in the application of water. It is important to realize that only a portion of the total water applied in irrigation is necessarily consumed in producing a crop. The water consumed and thus lost to the irrigated area is that used in the production of plant tissue (Briggs and Shantz water requirement), that transpired from the leaves, plus that evaporated from the soil and plant surfaces. This quantity of water which is actually consumed is commonly called consumptive use or evapotranspiration. "Water requirement" as often used in irrigation includes consumptive use plus an allowance for "normal" irrigation application losses. Thus, although this concept of water requirement is a very practical one, such values cannot be given for various crops without specifying irrigation efficiency. Because of this difficulty, "water requirement" will be used as defined by Briggs and Shantz. In connection with irrigation experiments, water use will be considered in terms of consumptive use.

II. WATER REQUIREMENT

The water requirement of plants is affected by numerous factors. This was shown in the classical investigations by Briggs and Shantz (1913a, 1913b, 1914, 1916a, 1916b, 1917) and Leather (1910). They brought out the importance of soil factors influencing water requirement, such as moisture content, soil type, soil compaction, soil fertility level, and the various climatic factors, especially those of temperature, humidity, and air movement. They and others have shown that practically any factor which affects plant growth also affects the water requirement to a greater or lesser extent. Most of the investigations conducted, however, have shown that of the various factors, climate is by far the most important. Table I is taken from Briggs and Shantz (1917) to show the effect of location on water requirement of the second crop of Grimm alfalfa at different stations in the Great Plains region.

TABLE I

Water Requirement of the Second Crop of Grimm Alfalfa at Different Stations in the Great Plains, 1912 (Briggs and Shantz, 1917)

Location	Growth Period	Days	Water requirement*	Evaporation (inches)	Daily evaporation (inches)	Ratio of water requirement to daily evaporation
Williston, N. D.	July 29– Sept. 16	47	518 ± 12	7.5	0.159	33
Newell, S. D.	Aug. 9–Sept. 24	46	630 ± 8	8.6	0.187	34
Akron, Colo.	July 26–Sept. 6	42	853 ± 13	9.5	0.226	38
Dalhart, Tex.	July 26–Aug. 31	36	1005 ± 8	11.0	0.306	34

* Expressed as grams of water per gram dry weight.

It will be noted from this table that the water requirement varied from 518 at Williston, North Dakota, to over 1000 at Dalhart, Texas, and that there is a close relationship between water requirement and evaporation in terms of inches. The ratio of water requirement to daily evaporation is rather constant, varying from 33 to only 38 for the entire area covered. Involved, however, in the data of Table I, may be any of the various soil or climatic factors which affect the water requirement.

Montgomery and Kiesselbach (1912) measured the water requirement of corn as influenced by fertility levels. Table II shows some of their data. Observe that there is a marked reduction in the water requirement with increasing soil fertility. Also of interest is the uniformity of water requirement data for the three soil types when manure was added.

Many of the data in the literature indicate that the effect of moisture level is not of great importance in affecting water requirement of plants. Scofield (1945), for example, found for three moisture levels—high, medium, and low—yields of 1105, 790, and 540 g. of dry weight per can with a corresponding water requirement of 781, 794, and 743.

Briggs and Shantz (1917) have shown large variations in water requirement by varieties of crops as well as very large differences among crops. For instance, they present data showing a variation of water requirement of less than 300 for Proso to over 1000 for western wheatgrass.

TABLE II

Water Requirement of Corn as Influenced by Soil Fertility, (Montgomery and Kiesselbach, 1912)

	Average dry wt. per plant (grams)		Water requirement* based on:			
			Total dry matter		Dry ears	
Soils	No manure	Manure	No manure	Manure	No manure	Manure
Infertile	113	376	550 ± 16	350 ± 8	2,136 ± 436	692 ± 45
Intermediate	184	414	479 ± 11	341 ± 4	1,160 ± 59	679 ± 36
Fertile	270	473	392 ± 6	347 ± 6	799 ± 39	682 ± 18

* Expressed as grams of water per gram dry weight.

Insofar as water use is concerned, however, it is not only the actual water requirement that is important but also the time of the year that the water is required and the ability of the plant to withstand dry conditions. The latter is particularly true in the dry-land areas of this country.

III. Consumptive Use

Although it is of importance to know the amount of water required to produce a unit of dry matter for various plants under different climatic conditions, it is of even more importance to know something of the total amount of water needed for crop production. The following items are involved: (1) Evapotranspiration or consumptive use and (2) irrigation losses including runoff and percolation. Runoff can be readily measured. In some instances, deep percolation can be measured by return flow to streams. The evapotranspiration is, of course, the most important of the three factors, since it is the one that is related directly to plants.

1. *Empirical Considerations*

Much work has been done on methods of estimating the evapotranspiration or consumptive use (Blaney and Morin, 1942; Blaney and Criddle, 1950; Penman, 1946, 1948, 1949, 1950, and 1951; Schofield, 1950 and 1952; Thornthwaite *et al.*, 1944; and Thornthwaite, 1948).

Blaney and Criddle (1950), for example, have carried on numerous investigations. In determining the consumptive use of water for large areas they have used the following formula: $U = KF$, where U equals the consumptive use of water in inches in any period, K equals an empirical constant, and F equals the sum of the monthly consumptive-use factors for the period (sum of the product of mean monthly temperature and monthly per cent of annual daytime hours).

In Blaney's and Criddle's use of the equation, K is determined experimentally. They give values of K for various crops grown in the irrigated West. According to them, the value of K usually varies only slightly. Typical values are shown in Table III.

TABLE III

Consumptive-Use Coefficients (K) for Irrigated Crops in Western States (Blaney and Criddle, 1950)

Crop	Length of growing season or period	Consumptive-use coefficient (K)*
Alfalfa	Between frosts	0.80–0.85
Beans	3 months	0.60–0.70
Corn	4 months	0.75–0.85
Cotton	7 months	0.60–0.65
Grains, small	3 months	0.75–0.85
Potatoes	3½ months	0.65–0.75
Rice	3–5 months	1.00–1.20
Sugar beets	6 months	0.65–0 75

* The lower values of K are for coastal areas; the higher values, for areas with an arid climate.

The net amount of irrigation water necessary to satisfy consumptive use is then found by subtracting the effective precipitation from the consumptive-use requirement for the irrigation season. This net requirement of irrigation water, divided by the irrigation efficiency, indicates the seasonal irrigation requirement for a given crop. The irrigation efficiency is defined as the ratio of the amount of water stored in the root zone × 100 divided by the total amount applied.

Van Bavel and Wilson (1952) indicate there is no great difference in the evapotranspiration rate of different crops under similar conditions. They say: "The work reported here is based on the assumption that a closed vegetation cover under equal meteorological conditions disposes of the soil water supply with equal rapidity, regardless of botanical composition." They report their data, using Thornthwaite's formula (Thornthwaite *et al.*, 1944, and Thornthwaite, 1948), on the daily evapotranspiration at Raleigh, North Carolina, and compare this to a running record of available soil moisture. They find the two to agree quite satisfactorily. They go on to state: "It is not proposed that adequate proof is supplied in favor of the evapotranspiration method; however, data to date are favorable and indicate that considerable more research should be done to determine its usefulness on different crops, soils, and areas."

Leather (1913) as early as 1913 gave an empirical formula for relating evaporation from a free water surface to temperature and dryness of the atmosphere and to wind velocity. He found this formula to agree with his observed records.

Penman (1948, 1951) has proposed a maximum evaporation from a free water surface based on an energy balance concept. He concludes that the maximum evaporation from wet soils and from turf with an adequate water supply is obtained as fractions of that from open water. The fraction for turf shows a seasonal change attributed to the annual cycle of length of daylight. In Penman's evaporation from turf, he includes evaporation and transpiration, or consumptive use. He has shown variations for the fraction of subirrigated grass to be from 0.6 to 0.8 in a 10-month period.

Penman's calculations involve the use of the following: (1) total monthly radiation estimated from hours of bright sunshine by Ångström's formula, (2) mean monthly air temperature, (3) mean monthly dew point temperature, and (4) mean wind speed; from there, he has estimated the evaporation from open water.

Based on Penman's method, Schofield (1952) has proposed to control the irrigation of grass from weather data and suggested this procedure might apply to other crops. He states that the maximum "evaporation," or consumptive use, depends on the weather and particularly on the amount of incident solar radiation and scarcely at all on the nature of the vegetation, so long as it is green. Under effective irrigation, he believes "evaporation" is at or near the maximum and can be computed from weather data. He points out that in England the Meteorological Service issues an estimate for maximum evaporation from crop land as a guide to irrigation based on Penman's method, and suggests such a service for this country.

2. *Experimental Field Data*

As indicated above, climatic factors are thought to have the greatest influence on consumptive use. Whether or not it will be possible to predict irrigation needs for maximum crop production on such data remains to be seen. An experiment conducted in Yuma, Arizona (Stanberry, C. O., Converse, C. D., and Haise, H. R., 1951, unpublished data), gives some interesting information on this subject. The experiment had the following three moisture levels: (1) wet treatment: the soil moisture tension to be maintained between field capacity and 175 cm. water tension at the 12-in. depth; (2) medium treatment: soil moisture tension to be maintained between field capacity and 600 cm. of water tension at the 18-in. depth; (3) dry treatment: plants allowed to wilt before each irrigation. This approximated 800 cm. water tension at the 36-in. depth. Combined factorially with these were several phosphorus levels, including an initial application of 100, 200, 400, or 600 lb. of P_2O_5 per acre. During the years of 1950 and 1951 the total amount of water used (consumptive use) was 184 in. for the wet, 158 in. for the medium, and 156 in. for the dry treatment. The dry plots used 85 per cent as much water as did the wet plots; thus the moisture level in this experiment had little effect on consumptive use. The alfalfa was green in all cases throughout the year. The fertility level had little or no effect on the total water used within a moisture level, but there was some differential stress developed between fertility plots. Had the fertility plots been irrigated individually for the moisture levels, there may well have been a slight difference in total water use for the fertility levels. In spite of the lack of large differences in consumptive use, the moisture levels greatly influenced the yields of alfalfa hay. Table IV gives the cumulative hay yields for over a three-year period.

Observe that the three-year average yield of the wet plots was 33.6 tons per acre as compared to 26.0 tons per acre on the dry plots. This is an increase of 7.6 tons per acre for the three-year period. The important comparisons, however, are those within both moisture and fertility levels. The yield for the three-year period for high phosphorus on the wet plots was 38 tons per acre as compared to 29.1 tons per acre for the dry plots. This was an average difference of 3 tons per acre per year and is as much or more alfalfa than is produced in the whole year in many areas. The total consumptive use was not greatly different, but the yield differences are remarkable.

Although it may be possible to estimate the total amount of water to be used by a given crop, much information is needed on when to apply it and how much to apply, and on the stresses which can be allowed to develop between irrigations. In this country we have a limited amount of water. We must, therefore, aim at the maximum production from what we have. Let us look at the rates of water used to tons of

TABLE IV

The Effect of Moisture and Phosphorus Levels on Tons of Hay per Acre Produced at Yuma, Arizona. Cumulative Yield for 1949, 1950, and 1951 (Stanberry, Converse, and Haise, Unpublished Data from Yuma Mesa Soil and Crop Laboratory, Yuma, Arizona, 1952)

Pound P_2O_5 per acre	Tons per acre (3 years)				
	Wet*	Medium†	Dry‡	Average	Relative
100	27.3	24.3	21.8	24.5	100
200	32.0	25.8	24.3	27.4	112
400	36.6	31.1	28.7	32.1	131
600	38.0	33.1	29.1	33.4	136
Average	33.6	27.6	26.0	29.3	
Relative	129	106	100	—	

* Treatment: The soil moisture tension to be maintained between field capacity and 175 cm. water tension at the 12-in. depth.

† Treatment: Soil moisture tension to be maintained between field capacity and 600 cm. of water tension at the 18-in. depth.

‡ Treatment: Plants allowed to wilt before each irrigation. This approximated 800 cm. water tension at the 36-in. depth.

TABLE V

The Amount of Water in Inches Required to Produce One Ton of Hay for Various Moisture and Fertility Treatments at Yuma, Arizona, in 1950 and 1951 (Stanberry, Converse, and Haise, Unpublished Data from Yuma Mesa Soil and Crop Laboratory, Yuma, Arizona, 1952)

Pounds P_2O_5 per acre	Inches of water per ton of hay				
	Wet*	Medium†	Dry‡	Average	Relative
100	10.67	11.60	12.81	11.69	152
200	8.79	9.11	10.49	9.46	123
400	7.45	8.20	8.80	8.15	106
600	6.82	7.45	8.86	7.71	100
Average	8.43	9.09	10.24		
Relative	100	108	121		

* Treatment: The soil moisture tension to be maintained between field capacity and 175 cm. water tension at the 12-in. depth.

† Treatment: Soil moisture tension to be maintained between field capacity and 600 cm. of water tension at the 18-in. depth.

‡ Treatment: Plants allowed to wilt before each irrigation. This approximated 800 cm. water tension at the 36-in. depth.

alfalfa hay produced in the above experiment. Table V gives this information.

These data show that the dry plots required more water to produce 1 ton of hay than did the wet plots. Relatively speaking, the dry plots required 21 per cent more water per ton of hay than did the wet plots, and the low-fertility plots required 52 per cent more water per ton of hay than the high-fertility plots.

If it is assumed that the most economical water treatment was the wet plot with 600 lb. of P_2O_5 per acre, Table VI gives the relative water use per ton of hay for the various treatments (Stanberry, C. O., Haise, H. R., and Converse, C. D., 1952, unpublished data).

TABLE VI

The Relative Amount of Water, Based on the High Yielding Plot, Required to Produce One Ton of Hay as Affected by Moisture and Fertility Level at Yuma, Arizona, in 1950 and 1951 (Stanberry, Converse, and Haise, Unpublished Data from Yuma Mesa Soil and Crop Laboratory, Yuma, Arizona, 1952)

Pounds P_2O_5 per acre	Wet*	Medium†	Dry‡
100	156	170	188
200	129	134	154
400	109	120	129
600	100	109	130

* Treatment: The soil moisture tension to be maintained between field capacity and 175 cm. water tension at the 12-in. depth.

† Treatment: Soil moisture tension to be maintained between field capacity and 600 cm. of water tension at the 18-in. depth.

‡ Treatment: Plants allowed to wilt before each irrigation. This approximated 800 cm. water tension at the 36-in. depth.

It is noted that the dry plot of low fertility required 88 per cent more water to produce 1 ton of hay than did the high-fertility plot in the wet treatment.

Fine, Erie, Campbell, and Dimick (unpublished data, Brookings, South Dakota), in a corn experiment at Redfield, South Dakota, during 1951, found the consumptive use to be 17.7 in. if the crop was irrigated when the moisture content of the first foot of soil was depleted to about 50 per cent of the available water. However, consumptive use was only 12.7 in. when the first foot of soil was allowed to drop to the point of 85 per cent depletion. No differences in corn yields were obtained. For alfalfa, the consumptive use was 24.4 and 20.5 in., respectively, for a depletion of 50 per cent and 85 per cent of available moisture for the first 2 feet of soil, but again, no yield differences were obtained.

Data by Haise, Olsen, and Jensen (unpublished) in 1951, working with alfalfa, obtained consumptive use figures of 25.3 in., 22.4 in., and 16.9 in. for three moisture treatments at Mandan, North Dakota. These three treatments were approximately 35 per cent depletion and 65 per cent depletion in the upper 4 ft. of soil with the third treatment being irrigated when the plants showed signs of moisture stress. There were no yield differences at Mandan. At Bowbells, with the same moisture treatments, yield differences were obtained between the dry and wet plots. Here, consumptive use was 18.0 in., 16.5 in., and 14.7 in., respectively.

Hanks and Tanner (1952), working with corn and oats in Wisconsin, show the effect of fertility level on water use. Table VII gives some of these data. They found that in every comparison there was more efficient use of water under the high-fertility treatments. In 1949 and 1950, corn yields per inch of water used were on the average 1.4 times greater on the high-fertility plots than on low-fertility plots. Similarly, oat yields per inch of water were 1.7 times greater on the high-fertility treatments than on the low-fertility treatments.

TABLE VII

Yield of Corn and Oats per Inch of Water as Influenced by Soil Fertility (Hanks and Tanner, 1952)

		Corn Yields in Bushels per Inch of Water			
		Irrigated		Not irrigated	
		Nitrogen level		Nitrogen level	
Crop	Year	High	Low	High	Low
Corn	1949	3.8	2.8	3.5	3.1
	1950	3.9	2.5	3.6	2.2
Oats	1949	4.4	2.3	4.3	1.2
	1950	3.7	2.8	3.6	2.4

The experiments referred to above can be summarized with respect to similarity of results as follows:

1. Effect of moisture level on consumptive use:
   - *a.* Yuma—Alfalfa, 17 per cent more water used on the wet plots than on the dry.
   - *b.* Redfield—Corn, 28 per cent more water used on the wet plots.

    - *c.* Redfield—Alfalfa, 16 per cent more water used on the wet plots.
    - *d.* Mandan—Alfalfa, 33 per cent more water used on the wet plots.
    - *e.* Bowbells—Alfalfa, 18 per cent more water used on the wet plots.

2. Effect of fertility level on efficiency of water use:
    - *a.* Yuma—high fertility increased efficiency of water use.
    - *b.* Data of Hanks and Tanner—high fertility increased efficiency of water use.
    - *c.* Redfield, Mandan, and Bowbells—No yield differences; therefore no effect of fertility treatment on water use.
3. Effect of moisture level on efficiency of water use:
    - *a.* Yuma—Alfalfa, yield responses were obtained; wet plots gave greater efficiency.
    - *b.* Hanks and Tanner—Corn, oats—yield responses were obtained; wet plots gave greater efficiency.
    - *c.* Bowbells—Alfalfa, yield responses were obtained; wet plots gave greater efficiency.
    - *d.* Redfield—Corn, yield responses were not obtained; wet plots gave less efficiency.
    - *e.* Redfield—Alfalfa, yield responses were not obtained; wet plots gave less efficiency.
    - *f.* Mandan—Alfalfa, yield responses were not obtained; wet plots gave less efficiency.
4. Agreement of consumptive use determined experimentally and calculated by Blaney and Criddle (1950) method.
    - *a.* Yuma—Blaney-Criddle consumptive use approximated the dry plots but 28 per cent too low for wet plots.
    - *b.* Bowbells—Blaney-Criddle method 30 per cent too high.
    - *c.* Mandan—Blaney-Criddle method 40 per cent too high.

The total amount of water needed and the time of year when it is required depend on the kind and amount of crop grown, its stage of growth, the soil and climatic conditions. In hot. dry climates with long seasons of growth, considerably more water is required than is necessary where the climate is more temperate and the growing season shorter. Perhaps the greatest single factor influencing the water needs of a farm is the soil. In theory, at least, the water needs of a crop grown on light, sandy soil should be no greater than if it were grown on a heavy clay. However, on sandy soil waste is usually larger because of high infiltration rates, and thus the irrigation efficiencies are often low.

The soil acts as a reservoir in which water is stored between irrigations for crop use. Both the total amount of water stored and the amount available to plants varies. Since the storage capacity and the available water are low for sands, the sands may have to be irrigated more frequently. This combination of more frequent irrigations with lower irrigation efficiency may result in excessive water use on a given field or farm. Extremely heavy soils also may have a similar effect on the amount of water required. This is particularly true if the infiltration rate is low. In some silt soils of the West the infiltration rate is so low that water has to be maintained on the soil for a long period of time in order to allow ample water to permeate the soil. If this type of soil has any appreciable slope and is irrigated by gravity, it is necessary that water run across the soil for long periods of time. Thus, the actual farm or field requirement of water may be extremely high.

IV. Availability of Soil Water

The availability of soil water to plants is affected by at least three main factors: (1) soil, (2) plant, and (3) weather. The weather factors have been discussed previously under Section III.

1. Soil Factors

The amount of water stored in the soil and available for plant use is determined primarily by the texture, structure, depth, and uniformity of the soil. Stratification in fine-textured soils, of course, may markedly affect water storage. These same factors are largely responsible for determining soil moisture stress relationships. Soil moisture stress is the sum of the soil moisture tension plus the osmotic pressure of the soil solution (Wadleigh, 1946). The relationship between soil moisture tension and percentage of moisture in the soil is given in Fig. 1 for three soils (Kelley *et al.* 1946). These curves show the diversity that can be associated with varying soil conditions. The Chualar loam and the Coachella loamy sand both contain approximately an equal amount of available moisture. Field capacity for the Chualar loam is around 16 per cent with a wilting percentage of 6.5, leaving about 9 per cent available water. The Coachella loamy sand has a field capacity of around 11 per cent with a wilting percentage of around 2 per cent, leaving available about 9 per cent moisture. It is readily seen that for the Chualar loam as the moisture content diminishes from field capacity, the moisture tension increases. This, however, is not true for the Coachella loamy sand. It will be noted that, as the moisture content decreases from around field capacity, there is a very small increase in moisture tension and that practically all the available moisture has been used by the time the soil moisture tension reaches 1 atm. If there is a differential response to plant growth within the available moisture range, then one would expect that plants grown on these two soils at varying moisture contents would behave differently.

The salt content of soils is of major importance in the arid West in determining the total soil moisture stress. Wadleigh *et al.* (1946) have shown the importance of the effect of salinity upon total soil moisture stress. They were working with a soil in which the field capacity was approximately 20 per cent and the 15 atm. value 8.6 per cent. They had two moisture treatments, one being designated as L, low moisture tension, which required that the soil be irrigated with sufficient water to bring the content to field capacity when the average soil

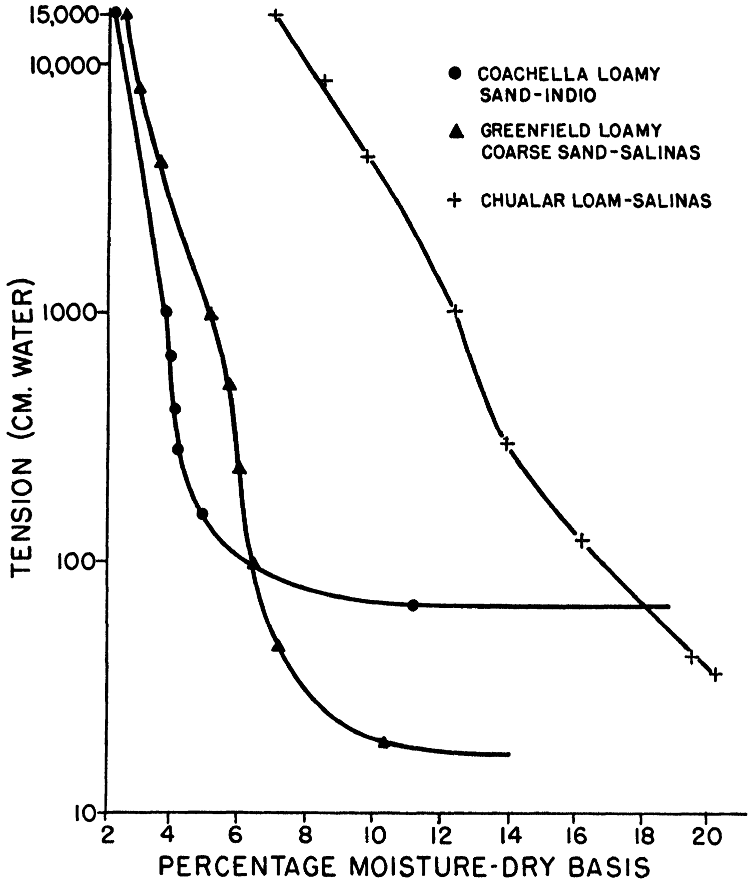

Fig. 1. Moisture retention curves for three soils.

moisture reached 14 per cent. This was equivalent to about 300 to 400 cm. of water at the 4-in. depth of soil. Their moisture treatment with a high tension, designated as H, was to be irrigated with sufficient water to bring the soil moisture content to field capacity when the average moisture content of a culture reached 9 per cent. This was approximately the 15 atm. value. In combination with these two moisture levels they had the following treatments:

Salt treatment (All salt added on dry soil basis)	Designation
No added salt	O
0.1% NaCl	C_1
0.2% NaCl	C_2
0.4% NaCl	C_4
0.2% Na_2SO_4	S_2
0.4% Na_2SO_4	S_4
0.8% Na_2SO_4	S_8

Through very frequent sampling of the soil they were able to obtain the osmotic pressure of the soil solution. They then mathematically computed the average or integrated soil moisture stress to which the plants were subjected in the growing period. Figure 2 shows the relationship between the average moisture stress of the irrigation interval and (1) to growth of the guayule plants and (2) the percentage of rubber in the millable bush (Wadleigh *et al.*, 1946). From the figure it is shown that the growth of guayule was closely related to the total moisture stress, regardless of whether this stress was due predominantly to soil moisture tension or osmotic pressure of the soil solution. The percentage of rubber in the millable bush was also found to be closely related to the average moisture stress over an irrigation interval. Here again, it was immaterial to rubber accumulation whether this moisture stress was induced by tension or by osmotic pressure. It is noted that when an average moisture stress exceeded 6 atm. it was progressively deleterious to rubber accumulation. In the nonsaline areas of the East, osmotic pressure of the soil solution is not so important.

Another soil factor of primary importance in determining the amount of water available to plants is the presence of a water table. The water table can be of sufficient height to prevent optimum growth or it can be low enough not to interfere with aeration but to provide water for deep-rooted plants in such a manner that it may well be beneficial. Various studies have been conducted showing a reduced irrigation requirement with a water table sufficiently close to the surface to provide some water for plant growth.

Soils containing hard pans or areas of high density relatively close to the surface may interfere with root penetration and thus affect the availability of water at lower depths. This is particularly true for plow layers or compacted layers that may develop close to the surface owing to tillage operations. In unpublished data obtained by Hunter and Kelley at Salinas, California, a very compact layer was found at 12 in. owing to tillage operations. The volume weight of this layer varied from 1.85 to 2.08 as compared to 1.60 for surface soil. Very few plant roots penetrated this zone, but once they did and dried the soil below this depth it was difficult if not impossible to rewet the lower depths at time of irrigation. Layers of this type have a profound effect upon the availability of water to plants at depths below such compacted zones.

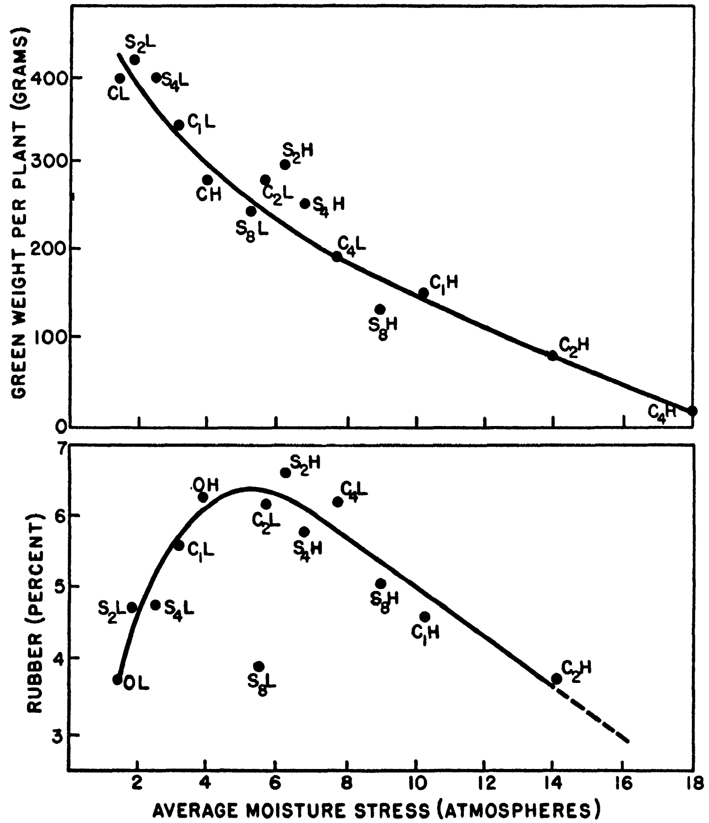

FIG. 2. The effect of moisture stress on growth and rubber content of guayule (Wadleigh and Gauch, 1946).

2. *Plant Factors*

The primary plant factors affecting the availability of water to plants are (1) rooting characteristics and (2) ability of the plant to withstand moisture stress.

Weaver (1926), Weaver and Bruner (1927), and Kramer (1949) have given information on plant root distribution both with respect to depth and ramification. Although the depth of root penetration is of major importance, so also is ramification. Some crops like sweet clover have a relatively shallow root system but rather completely ramify the soil. Figure 3 shows a moisture extraction pattern obtained by Hagan and Peterson (unpublished data, Davis, California) for ladino clover at time of wilting at Davis, California. The available water was nearly all used to a depth of 12 in. Over 70 per cent was used from the 12- to 18-in. depth and only 57 per cent from the 18- to 24-in. depth. No measurable amount of water was used below the 24-in. depth. Other crops such as potatoes, celery, and onions may have some roots which penetrate to the 24-in. depth or lower, but seldom do their roots permeate the entire soil mass to any great extent. Most of the roots are close to where the seed was planted and in many cases even in the first

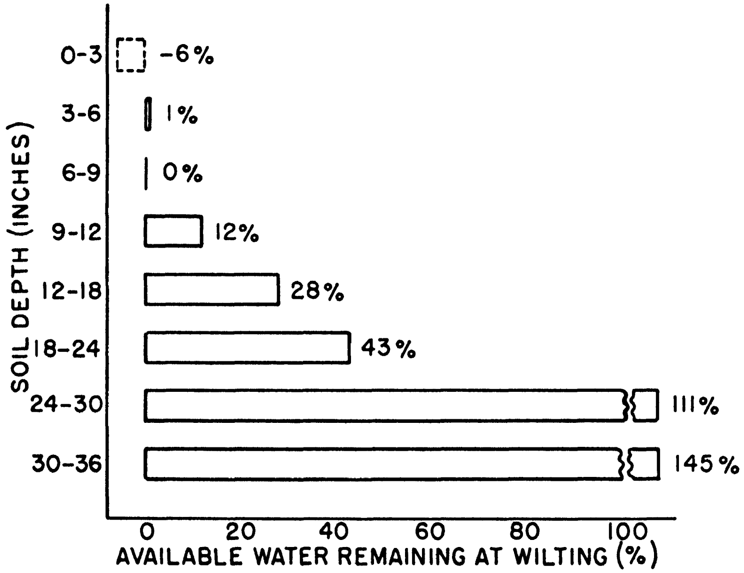

FIG. 3. Water extraction by ladino clover at time of wilting (Hagan and Peterson, unpublished data, Davis, California).

12 in. of soil all of the available water is not removed before the plants show moisture stress. Veihmeyer and Holland (1949) have shown this is also true for lettuce.

On the other hand, such crops as wheat, barley, rye, and many perennial plants may have root systems that extend to great depths. The importance of the depth of rooting is related to availability of moisture of the soil profile, the ramification of roots at the lower depths, and the presence or absence of a water table. Bowen (1938) has given some interesting data on the use of water by crops as related to soil depth when the soil profile was kept relatively well supplied with moisture. Some of his data are given in Fig. 4. From the graphs indicating the depths from which the moisture is extracted, we see that the greatest moisture change occurs in the upper 2 to 3 ft. of soil. With all crops

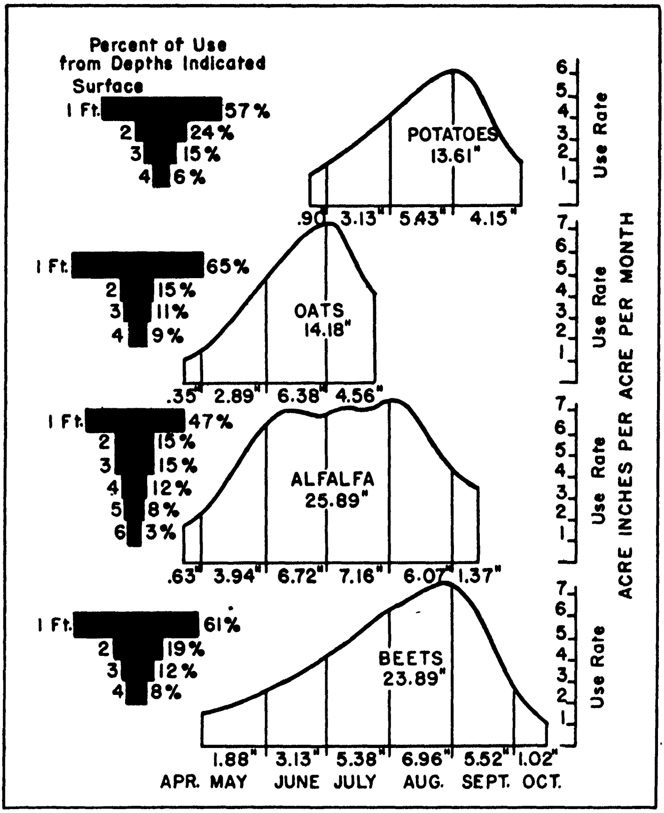

FIG. 4. Moisture extraction pattern for various crops at Scotts Bluff, Nebraska (Bowen, 1938).

except alfalfa, fully 80 to 90 per cent of the total water is taken from the upper 3 ft. Even in the case of alfalfa, over 75 per cent of the water was obtained from the upper 3 ft. Of considerable interest are his data on sugar beets. Sugar beets are often thought of as being a deep-rooted crop. Doneen (1942) found that under certain California conditions the soil could be allowed to dry to the wilting percentage at 4 to 5 ft. without reducing sugar production. In the work by Bowen, his data indicate that over 60 per cent of the moisture obtained by beets at Scotts Bluff was in the first foot of soil. Only 8 per cent was obtained below the 3-ft. depth, and no measurable amount was used by the beets below the 4-ft. depth.

The ability of crops to withstand soil moisture stress for even a short duration is of great importance in nonirrigated areas, especially in the dryer regions. Sorghum is an excellent example of a crop which can be subjected to a considerable moisture stress and then renew growth when moisture is available. Alfalfa and some of the grasses have this ability to a lesser extent. In most cases such crops as celery, potatoes, and lettuce will not withstand any appreciable soil moisture stress without drastically affecting plant growth and quality. Kelley *et al.* (1945) have shown that guayule will withstand long periods of drouth and renew growth. Hendrickson and Veihmeyer (1931) have shown that Thompson seedless grapes have the ability to withstand high soil moisture stresses.

V. CONFLICTING CONCEPTS OF SOIL MOISTURE AVAILABILITY

Numerous investigations have been made in the subject of how water should be maintained in the soil for maximum growth. As a result of these many investigations, at least two general concepts have arisen. One is well stated by Veihmeyer and Hendrickson (1934) as follows: "Our studies with grape vines, peach, prune, apricot, apple, and pear trees in field plots and containers, and with sunflowers, show there is no one percentage of moisture above the permanent wilting percentage at which plants grow better than at any other and which, therefore, could be considered optimum for plant growth."

The other is the belief that all soil moisture above the wilting percentage is not equally available to plants. A thorough review of the literature on this subject was recently made by Richards and Wadleigh (1952), and, therefore, no attempt will be made to review the numerous investigations made on this subject.

However, since this subject is of so much interest to agronomic workers a few typical investigations are summarized in Table VIII. Most of the data summarized in Table VIII show that all water above the wilting percentage is not equally available, in terms of maximum plant growth. In cases where there apparently is no difference, there may be several reasons:

1. It was pointed out in Fig. 1 that light-textured soils hold most of their available water at a low tension. Experiments conducted in these soils cannot have large differential tension effects on plant growth for any appreciable periods of time if the soil moisture is maintained within the available range. For instance, if 80 to 90 per cent of the available water is held at tensions less than 1 atm., then only 10 to 20 per cent is available from 1 atm. to 15. If water extraction proceeds at about the same rate throughout the available range, as indicated by Veihmeyer (1927), then the plants would be growing under soil moisture stresses greater than 1 atm. for only 10 to 20 per cent of the time. The possibility of determining the effect of variations in soil moisture tension is greater in soils similar to the Chualar loam (Fig. 1), where there is an appreciable change in tension with a change in moisture content throughout the available moisture range.

2. Much of the work was done on a soil-moisture sampling basis with no relation to soil-moisture stress. The errors involved in soil-moisture sampling in many cases amount to at least 10 per cent of the available range. In the dry range this represents an appreciable change in tension.

3. In some cases experiments have been conducted with deep-rooted plants which extend to depths of 6 to 20 ft. In many of these cases soil moisture was not followed throughout the root zone, and hence the moisture condition at the lower depths was not known.

Even where moisture has been studied on a stress basis, seldom has the mean stress over the entire root system been known. Taylor (1952) has recently developed a method for integrating soil moisture tension in the root zone under growing crops. He obtains a mean soil moisture tension of a single value for the entire growing season or any portion thereof; this should aid greatly in the interpretation of future studies.

4. Climatic factors may affect the results obtained. It is to be expected that plant growth responses to differential moisture stress conditions would be small in climates where transpiration rates are low.

In the extensive review of literature by Richards and Wadleigh (1952) they summarize their interpretations of numerous experiments as follows: "From the irrigation and soil moisture experiments mentioned in the foregoing section it is apparent that there is considerable evidence that significant differences in growth rates occur along with varying degrees of moisture depletion within the so-called available moisture range * * * . Throughout the moisture depletion process the

TABLE VIII

Growth and Yield of Crops in Relation to Soil Moisture*

Reference	Place	Crop	Soil	Nature of investigations	Results or conclusions
Hendrickson & Veihmeyer (1929)	San Joaquin Valley, Calif.	Peach	Oakley fine sand. Moisture equivalent 2.6–6.2%.	Field experiment, 6 irrigation practices. *A*. Kept above permanent wilting percentage, others had varying dry periods based on water in upper 3 ft.	Yield over 4 years: *A*. Above permanent wilting percentage 944 bu. largest trunk *B*. Frequent dry periods 868 bu. intermediate trunk *C*. Long dry periods 734 bu. smallest trunk
Hendrickson & Veihmeyer (1931)	San Joaquin Valley, Calif.	Grape	Fresno sandy loam. Moisture equivalent 9–11%; permanent wilting percentage 3–4.	Field experiment, irrigation. *A*. Moisture kept above permanent wilting percentage in first 5 ft. *B*. Reduced to permanent wilting percentage twice. *C*. Reduced to permanent wilting percentage last part of season.	Size of fruits largest under *A*, smallest under *B*, but differences were small and considered insignificant.
Hendrickson & Veihmeyer (1934)	Davis, Calif.	Prunes	Yolo loam. Moisture equivalent 14–20%; permanent wilting percentage 8–10.	Field experiment 10 years. *A*. Ample moisture. *B*. Irrigated to July 1. *C*. Irrigated after July 1. *D*. No irrigation.	Trunk increase Yield cumulative *A*. 425 sq. cm. 1180 bu. *B*. 377 sq. cm. 1080 bu. *C*. 373 sq. cm. 1000 bu. *D*. 325 sq. cm. 815 bu. Only difference between *A* and *D* significant.

Hendrickson & Veihmeyer (1942)	Various places in Calif.	Apples Pears Peaches	Yolo loam. Moisture equivalent 21–24%; permanent wilting percentage 10–12.5.	Field experiment compared ample water with allowing soil to reach permanent wilting percentage in upper 3 ft.	Pears in Hollister area showed no change in fruit volume. Pears in Contra Costa County fruit size reduced by low moisture. Apple no difference in fruit size.
Lewis, Work & Aldrich (1934)	Rogue River, Ore.	Pears	Meyer silty clay loam. Meyer adobe clay. Field capacity 23–25%; permanent wilting percentage, 13–16.	Field experiment. Irrigations *E*. 80% available water maintained. *D*. 50% available water maintained. *B*. 20% available water maintained. *C*. As owner.	Yield — Fitch — Klamath *E*. 1114 lb. 1514 lb. *D*. 582 lb. 1161 lb. *B*. 537 lb. 570 lb. *C*. 292 lb. 509 lb. Rate of growth and size and quality of fruit closely related to moisture in soil.
Work & Lewis (1936)	Rogue River, Ore.	Pear	Clay soil. Permanent wilting percentage, 14–18.	Studied moisture loss and root distribution.	Rate of moisture loss decreases before permanent wilting percentage was reached because roots do not fully occupy soil mass.
Furr & Taylor (1939)	Southern Calif.	Lemon	Various.	Field tests, moisture in soil determined and related to fruit size, moisture in leaves, etc.	As soil moisture decreased tree turgor decreased. Fruit size decreased before wilting occurred. When fruit lost moisture, water in root zone varied from wilting percentage to near field capacity.
Anderssen (1951)	South Africa	Oranges			Allowing the trees to show wilt at 9:00 A.M. reduced yields as compared to trees irrigated sufficiently and frequently to prevent wilt.

TABLE VIII (*Continued*)

Reference	Place	Crop	Soil	Nature of investigations	Results or conclusions
Veihmeyer (1927)	Davis, Calif.	Prune trees, young	Yolo clay loam. Moisture equivalent 22%; permanent wilting percentage, 12%.	Outdoor tanks 23–27 in. diameter, 48–72 in. deep. Soil allowed to reach certain minimum moisture percentage.	Min. soil moisture % — Length growth — No. leaves 16 — 518 in. — 655 12 — 417 in. — 543 Use of water not influenced by water above permanent wilting percentage. Concluded also that tree growth not affected by moisture above permanent wilting percentage.
Peterson (1952)	Logan, Utah	Sweet corn	Nibley clay loam.	Field experiments. Soil moisture. Moisture controlled on tension basis Wet Medium Dry	Corn yield, tons: No N — High N; Stover, tons: No N — High N 3.32 — 8.20 — 7.4 — 22.3 3.05 — 5.70 — 5.8 — 16.0 3.07 — 5.66 — 5.9 — 11.5
Miller & Duley (1925)	Columbus, Mo.	Field corn		Greenhouse in containers having 400 lb. soil	Plant growth suffered more during early periods than late from inadequate moisture. Corn grain yield varied closely with moisture supply in soil during last 30 days of growth.
Howe & Rhoades (1948)	Scotts Bluff, Neb.	Potatoes	Tripp very fine sandy loam.	Field experiment. Irrigate at following moisture tensions 200 mm. Hg at 6 in. 400 mm. Hg at 6 in. Res. blocks 100,000 ohms, 6 in.	Total yield, bu./acre — U.S. No. 1, bu./acre 550 — 125 470 — 80 448 — 31

Oppenheimer (1951)	Palestine	Corn grain			A twofold increase was obtained for plots maintained wet as compared to those that were allowed to wilt before irrigation.		
Morgan (1949)	Victoria, Australia	Clover			Increased clover production with frequent light irrigations. Allowing clover to wilt reduced production.		
Makkink (1945, 1948)	Netherlands	Grassland			Crop yields were reduced by allowing wilting. More frequent irrigation increased grassland production. Excessive irrigation reduced yield.		
Adams, Veihmeyer, & Brown (1942)	San Joaquin Valley, Calif.	Cotton, Acala	Panoche adobe. Moisture equivalent 30–35%; permanent wilting percentage, 16–18.	Field test	Water applied (in.)	Plant height (in.)	Seed cotton (lb./plant)
				1932			
				W_1 irrigate when ½ water available gone.	19.2	24.0	0.19
				W_2 irrigate first wilting (no irrigation).	0.0	17.5	0.09
				W_5 irrigate July 22 & 3 later irrigations.	15.9	25.0	0.23
				1934			
				W_1 irrigate when ½ water available gone.	42.8	32.5	0.28
				W_2 irrigate before permanent wilting percentage in first foot.	25.5	29.5	0.28
				W_3 allow severe wilting.	13.5	23.6	0.26

TABLE VIII (*Continued*)

Reference	Place	Crop	Soil	Nature of investigations	Results or conclusions	
Beckett & Dunshee (1932)	Shafter, Calif.	Cotton, Acala	Delano sandy loam.	Field test:	Plant height (in.)	Seed cotton (lb./plant)
				Irrigate when 5 ft. soil is 7% moisture	48.0	55.8
				Irrigate when plants wilt 4:00 P.M.	39.3	41.4
				Irrigate when plants wilt 9:00 A.M.	35.6	32.6
					Increasing deficiency of water decreased growth.	
Harris & Hawkins (1942)	Salt River Valley, Ariz.	Cotton	Field capacity 16.7%; permanent wilting percentage 8.0.	Field test:	Yield of seed cotton (lb.)	
				Irrigate at 12% in 1st foot	1,811	
				Irrigate at 8% 1st irrigation, 12% thereafter	1,209	
				Irrigate at 9.5%	1,334	
				Irrigate at 8%	1,105	
Kelley, Hunter, & Hobbs (1945)	Salinas, Calif.	Guayule	Chualar loam.	Field test with nursery plants:	Plant weights	
				Irrigate at tension:	(g.)	
				850 cm., 6 in.	272.6	
				850 cm., 12 in.	253.5	
				Permanent wilting percentage, 6 in.	236.3	
				Permanent wilting percentage, 12 in.	230.9	

Clements (1948)	Hawaii	Sugar cane	Clay. Field capacity 35–37%; permanent wilting percentage 24–25.	5 years studies.	When moisture dropped to 28% there was a reduction in growth.
Taylor (1951)	N. Logan, Utah	Sugar beets Potatoes	Millville loam.	Analysis of field data on Greenville farm. Irrigation experiment for relation between soil moisture tension and crop yields.	A straight-line function was found between increase in integrated tension and decrease in yield for each crop.

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* The author is indebted to Dr. D. W. Thorne, Utah State Agricultural College, Logan, Utah, for this table.

soil moisture stress increases continuously and much experimental evidence supports the hypothesis that the growth rate of various plants decreases markedly in the available soil-moisture range and that vegetative growth is completely inhibited by the time the soil moisture is depleted to the permanent wilting range."

VI. SUMMARY

Terminology used to describe water use is briefly summarized, and factors affecting water use by plants are discussed.

Methods for estimating consumptive use are considered. Data presented indicated considerable variation between values calculated using the Blaney-Criddle formula and experimental values for alfalfa at three locations.

Consumptive use varied with soil moisture level. The higher the average soil moisture level, the higher the value for consumptive use. However, at most locations, consumptive use for the wettest treatment did not exceed that for the driest by more than about 30 per cent.

The effect of soil moisture levels on the efficiency of water use by plants was conditioned by the influence of moisture levels on crop growth. Where yields were increased by maintaining a high soil moisture value by frequent irrigation, there was an increase in efficiency of water use by the crop. However, where there was no gain in crop yield with increased water applications, there was, in general, a decrease in the efficiency of water use.

Fertility level has a marked effect on the efficiency of water use by plants. Wherever higher yields were obtained with increased fertilizer usage, there was a corresponding increase in the efficiency of water use.

A discussion is given on the availability of soil water as affected by (1) soil conditions, (2) plant factors, and (3) weather. A brief review of the conflicting concepts of soil moisture availability is included.

REFERENCES

Adams, F., Veihmeyer, F. J., and Brown, N. 1942. *Calif. Agr. Expt. Sta. Bull.* **668.**

Anderssen, F. G. 1951. *Farming in S. Africa* **26,** 309, 491–495.

Beckett, S. H., and Dunshee, C. F. 1932. *California Agr. Expt. Sta. Bull.* **537.**

Blaney, H. F., and Criddle, W. D. 1950. *U. S. Dept. Agr.* SCS-TP-96.

Blaney, H. F., and Morin, K. V. 1942. *Trans. Am. Geophys. Union* **23,** 76–83.

Bowen, Leslie. 1938. *Agr. Eng.* **19,** 13, 14.

Briggs, L. J., and Shantz, H. L. 1913a. *U. S. Dept. Agr., Bur. Plant Industry Bull.* **230.**

Briggs, L. J., and Shantz, H. L. 1913b. *U. S. Dept. Agr., Bur. Plant Industry Bull.* **285.**

Briggs, L. J., and Shantz, H. L. 1914. *J. Agr. Research* **3**, 1–64.

Briggs, L. J., and Shantz, H. L. 1916a. *J. Agr. Research* **5**, 583–650.

Briggs, L. J., and Shantz, H. L. 1916b. *J. Agr. Research* **7**, 155–212.

Briggs, L. J., and Shantz, H. L. 1917. *Pan Amer. Sci. Congr. Proc.* **3**, 95–107.

Clements, H. F. 1948. *Repts. Hawaiian Sugar Technol., 6th Meeting.*

Doneen, L. D. 1942. *Am. Soc. Sugar Beet Technol. Ann.*, 54–62.

Furr, J. R., and Taylor, C. A. 1939. *U. S. Dept. Agr. Tech. Bull.* **640.**

Hanks, R. J., and Tanner, C. B. 1952. *Agron. J.* **44**, 98–100.

Harris, Karl, and Hawkins, R. S. 1942. *Arizona Agr. Expt. Sta. Bull.* **181**, 421–459.

Hendrickson, A. H., and Veihmeyer, F. J. 1929. *California Agr. Expt. Sta. Bull.* **479.**

Hendrickson, A. H., and Veihmeyer, F. J. 1931. *Proc. Am. Soc. Hort. Sci.* **28**, 151–157.

Hendrickson, A. H., and Veihmeyer, F. J. 1934. *California Agr. Expt. Sta. Bull.* **573.**

Hendrickson, A. H., and Veihmeyer, F. J. 1942. *Proc. Am. Soc. Hort. Sci.* **40**, 13–18.

Howe, O. W., and Rhoades, H. F. 1948. *Soil Sci. Soc. Amer. Proc.* **13**, 539–544.

Kelley, O. J., Hunter, A. S., Haise, H. R., and Hobbs, C. H. 1946. *J. Am. Soc. Agron.* **38**, 759–784.

Kelley, O. J., Hunter, A. S., and Hobbs, C. H. 1945. *J. Am. Soc. Agron.* **37**, 194–216.

Kramer, P. J. 1949. "Plant and Soil Water Relations." McGraw-Hill Book Company, New York.

Leather, J. W. 1910. *Mem. Dept. Agr. India, Chem. Ser.* **1**, 205–281.

Leather, J. W. 1913. *Mem. Dept. Agr. India, Chem. Ser.* **3**, 1–15.

Lewis, M. R., Work, R. A., and Aldrich, W. W. 1934. *U. S. Dept. Agr. Tech. Bull.* **432.**

Makkink, G. F. 1948. *Verslog. Cent. Inst. Landbouwk. Onderzoek*, 27–30.

Makkink, G. F. 1949. *Verslog. Cent. Inst. Landbouwk. Onderzoek*, 49–57.

Miller, M. F., and Duley, F. L. 1925. *Missouri Agr. Expt. Sta. Research Bull.* **76.**

Montgomery, E. G., and Kiesselbach, T. A. 1912. *Nebraska Agr. Expt. Sta. Bull.* **128.**

Morgan, A. 1949. *J. Dept. Agr. Victoria* **47**, 97–105.

Oppenheimer, H. R. 1951. *Palestine J. Botany, Rehovot Ser.* **8**, 32–45.

Penman, H. L. 1946. *Repts. Progr. in Phys.* **2**, 366–388.

Penman, H. L. 1948. *Proc. Roy. Soc. (London)* **A**, 193.

Penman, H. L. 1949. *J. Soil Sci.* **1**, 74–89.

Penman, H. L. 1950. *J. Inst. Water Engrs.* **4**, 67–69.

Penman, H. L. 1951. *Quart. J. Roy. Meteorol. Soc.* **74.**

Peterson, H. B. 1952. *Farm & Home Sci. (Utah Agr. Expt. Sta.)* **13**, 5, 23.

Richards, L. A., and Wadleigh, C. H. 1952. *Agronomy* **2** *(Soil Phys. Conditions and Plant Growth)*, 73–251.

Schofield, R. K. 1950. *Trans. Intern. Congr. Soil Sci., 4th Cong., Amsterdam* **1**, 20–28.

Schofield, R. K. 1952. *Proc. 6th Intern. Grassland Congr.* **1**, 757–762.

Scofield, C. S. 1945. *U. S. Dept. Agr. Circ.* **735.**

Taylor, S. A. 1951. *Farm & Home Sci. (Utah Agr. Expt. Sta.)* **12**, 50, 51, 61.

Taylor, S. A. 1952. *Soil Sci.* **73**, 331–339.

Thornthwaite, C. W., *et al.* 1944. *Trans. Am. Geophys. Union* **25**, 683–693.

Thornthwaite, C. W. 1948. *Geog. Rev.* **38**, 55–94.

Van Bavel, C. H. M., and Wilson, T. V. 1952. *Agr. Eng.* **33**, 417–420.

Veihmeyer, F. J. 1927. *Hilgardia* **2**, 125–290.

Veihmeyer, F. J., and Hendrickson, A. H. 1934. *Am. Soil Survey Assoc. Bull.* **15**, 76–80.

Veihmeyer, F. J., and Holland, A. H. 1949. *California Agr. Expt. Sta. Bull.* **711.**

Wadleigh, C. H. 1946. *Soil Sci.* **61,** 225–238.

Wadleigh, C. H., Gauch, H. G., and Magistad, O. C. 1946. *U. S. Dept. Agr. Tech. Bull.* **925.**

Weaver, J. E. 1926. "Root Development of Field Crops." McGraw-Hill Book Company, New York.

Weaver, J. E., and Bruner, W. E. 1927. "Root Development of Vegetable Crops." McGraw-Hill Book Company, New York.

Work, R. A., and Lewis, M. R. 1936. *J. Am. Soc. Agron.* **28,** 124–134.

A Pattern for International Collaboration in Agriculture

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I. INTRODUCTION AND PRINCIPLES

During the past fifty years it has become apparent that isolation of any part of the world is no longer possible. Modern improvements in communication, transportation, and other branches of science and technology have continuously tended to bring the countries of the world into closer and closer juxtaposition until today essentially the only barriers left between them are linguistic and political. Intercontinental travel, which was once limited to explorers, traders, missionaries, the military, and a few of the wealthy, is now practiced by thousands of ordinary citizens every year. International travel is today looked upon with the same nonchalance with which local travel was viewed two decades ago, and businessmen, professionals, and tourists representing almost every nation of the world can be found in any great capital city.

Unfortunately, but perhaps understandably, technical progress among the nations of the world has far outstripped social progress, and as a result many misunderstandings and difficulties have occurred. We are prone to think of the benefits of civilization as being synonymous with machines and tend to overlook those moral and spiritual values which should take precedence over the material ones. Consequently, major world progress today is manifest in the machines for modern living as well as in those for destruction. If it were possible to make similar rapid progress in international education and understanding, then perhaps the necessity for the development of the machines of war would disappear, and it would be possible to concentrate intellectual, moral, and physical forces on making the world a better and more peaceful place in which to live.

As the world's population has increased, the problems facing society have gone through considerable evolution. When there was sufficient land and adequate natural resources for all, it was believed by many that the greatest and most pressing problems facing society were those of public health. Today, however, it must be realized that one of the foremost problems confronting the world is that of an adequate food production for all of mankind. At the same time the fact must be faced that the world itself is growing no larger, although its population is increasing by leaps and bounds each year. The solution of this problem lies in two obvious directions, namely, increasing use of technology which will enable the world to produce more food more efficiently and take care of the growing population, and the application of knowledge which will lead toward the stabilization of the world population in order that it may not outstrip the world's resources.

In recent years it has become apparent that not only for humanitarian reasons but for reasons of self-interest as well, it is essential that those nations which have been most fortunate in their natural resources and their national development aid the other nations of the world to utilize their human and natural resources for the benefit of all. As this idea has developed and crystallized, a considerable number of diversified efforts have been initiated by governmental and private agencies in an effort to help those nations which are presently underdeveloped to take maximum advantage of their own resources and potentialities so that they themselves may assume a respected place in world society. As implied by the title, this paper is intended to discuss principles and to describe one type of pattern which might be applied in helping certain nations attain the stated objective.

In seeking to aid the underdeveloped nations of the world through technical collaboration in agriculture, in other natural sciences, or in social sciences, it seems that there are certain principles which should always be kept in mind. The world obtains no benefit from ill-advised, abortive, or poorly planned programs of international collaboration, and it is therefore essential to establish sound principles for the planning, organization, and execution of such programs and to embark upon them only when there is evidence that they may be successful and have mutually beneficial results.

One very important principle in planning any sort of technical assistance for a nation is to distinguish between need and opportunity. Important human needs are easily recognizable and readily demonstrable in many parts of the world, but real opportunities for the intervention of foreign agencies to alleviate these needs by the application of technical knowledge are not always so clearly defined. Compassion and good will are laudable virtues, but they can become dangerous if allowed to blind one to the fundamental problems which present themselves. It is dangerous as well as odious to talk about know-how as being the solution to the world's problems. Most commonly demonstrated human needs in a given area cannot be resolved simply through the application of so-called know-how by other nations, and when this is done without attempting to determine the true possibilities for useful technical assistance and without attacking local problems at their roots, either no benefits are obtained or they are only temporary and provide no final solution to these problems.

When need and opportunity have been clearly defined in relationship to each other, then it should be possible to develop sound programs and patterns for technical collaboration, with lasting benefits. Unfortunately, too often there may be a sense of urgency involved in such programs and heavy pressure to make maximum accomplishment in a minimum period of time. In principle this aim is laudable, but in practice it is often quite impractical. The same factors responsible for the lack of development of the country in question mitigate against the rapid solution of its problems. Only through a careful study of these factors and a program designed to take them into consideration in carrying out technical collaboration is it possible to produce accomplishments which will bring about continuing benefits to the nation concerned.

It is logical that any foreign technical aid program should be framed in terms of the needs of the country under consideration. To establish these needs clearly, it is necessary to spend both time and thought in preliminary surveys and in evaluation of current and long-range problems as well as possibilities for their solution. This means that competent individuals must travel widely in the country in question, consult extensively with leaders in the fields of agricultural science, education, extension, and production, and ascertain the thinking of the political and social leaders of the state. As this is done, problems become apparent and the desires on the part of the nationals of the country in question for collaboration in the solution will be expressed. Finally, there may be agreement on the over-all type of program to be initiated, those projects of greatest importance, and those of collateral emphasis, as well as details of organization.

In planning to provide technical aid abroad, it is important to keep in mind the economic and technical resources of the country involved. No foreign aid program should impose upon the recipient country greater economic expenditures than its budget will readily sustain. Neither should such a program contemplate early attainment of such size that it will very rapidly outstrip available national personnel who can be trained ultimately to take over the entire responsibility. It is very much better to initiate technical aid projects slowly and permit them to grow only as rapidly as accomplishments dictate. These should then be reviewed periodically and modified to suit changing conditions. The entire program should fit itself into the cultural pattern of the country in which it has been established and produce trained nationals who will take greater and greater responsibility for the further development of the projects. At some point the effort should become such an integral part of the over-all scientific agricultural activities in the country concerned that foreign technical aid is no longer urgently needed, and it will be possible to begin to withdraw with the assurance that the work will continue and expand under completely national auspices.

In the past it has been the practice of underdeveloped countries to borrow information and material from more advanced countries. This is a logical and natural procedure, but often it is not a successful one. Conditions which maintain in one country are not necessarily those which exist elsewhere, and as a result the importation of seeds and other plant materials and of agricultural techniques and information from one country to another is not always the best way to increase national agricultural production. However, through foreign technical aid it is possible to evaluate local conditions and to decide both the needs and the possibilities for the utilization of materials from other areas. Careful studies of altitude, rainfall, climate, soil fertility, disease and pest problems, and plant and animal varieties used for food production enable the scientist to decide where to turn for material which is likely to prove useful. Often he finds that it is possible to utilize, at least temporarily, varieties which have been developed elsewhere and to apply techniques for the control of pests and disease which have been found effective in other countries, as well as methods of soils management which in conjunction with these other activities make it possible to obtain immediate or early benefits to local agriculture. For best results agricultural improvement programs involve introduction and testing over a wide geographical range, as well as the early initiation of projects calculated to produce materials and methods of maximum utility under local conditions.

The true measure of the success of a program of international and technical collaboration is not in its accomplishments during the period it is in force, but rather in what happens after foreign aid has been withdrawn. Unless changes brought about are both permanent and dynamic and unless benefits continue to accrue in greater measure after the termination of the program, it cannot truly be considered as having been successful, and there is real doubt as to whether, under such circumstances, it should have been initiated at all.

Stability of policy and of support is an essential quality for the successful prosecution of a program of technical collaboration. Assuming that adequate planning has preceded the actual establishment of the program, individual projects should be initiated on a sound basis and should be permitted to develop normally and in response to opportunity and for such a period of time that successful, long-range accomplishments are in no wise sacrificed to either haste or expediency. The fact that there are underdeveloped countries in the world which need assistance from other nations is the best evidence that there are long-standing deficiencies in education, technology, and development which cannot be resolved on a short-term basis.

In the final analysis no program of foreign technical collaboration can possibly be successful unless the personnel assigned the responsibility for carrying on the work are of an appropriate caliber. Technical competence alone is insufficient and must be accompanied by an international viewpoint, a determination to learn local languages and customs, the ability to see local problems in their logical framework, and the willingness to work within this framework towards stated objectives. Recruitment of appropriate personnel is one of the most difficult tasks of technical collaboration in the foreign field. If urgency and expediency are substituted for a careful process of selection, eventually the disadvantages of this system will far outweigh the advantages of rapid recruitment to get approved projects under way.

Since individuals assigned to foreign programs of technical collaboration are inevitably ambassadors for the country they represent, the success or failure of the effort rests largely upon their shoulders both as technicians and as individuals. Thus it is essential always to seek persons who from the standpoints of training, experience, ability, and personality offer greatest promise of success in their foreign assignments. Since such persons are not in excess supply in any country, when they are found they can only be attracted by the assurance of an opportunity for real service in international development as well as reasonable guarantees of stability, opportunities for advancement, and agreeable conditions for family life.

The greatest contribution which any foreign technical aid program can make does not lie in the technical accomplishments themselves, but rather in its total impact upon the people of the nation concerned. They must first become convinced that the program is one of good will and of real value; that foreign operating personnel desire to become a part of the community in which the program is being carried out; that empire-building is not contemplated; and finally, and most important, that there is definite and sustained effort to transfer knowledge and skills imported from other countries to the nationals of the country benefited. Only then will there be general acceptance of the results obtained and will these be applied to the amelioration of local conditions.

The formal and informal training of young nationals of countries involved in technical collaboration programs is the most vital single factor in this type of effort. Admittedly, this must sometimes be started at a very elementary level, often with many delays and discouragements attendant upon the situation encountered. Nevertheless, every national who receives training through the application of technical collaboration becomes one more person who may devote his life and efforts and abilities to the solution of the important problems of his country. The number and the competence of such individuals developed by a technical collaboration program will in the long run determine the total success of the operation.

There are several ways of helping to train the nationals of those countries in which technical collaboration is practiced. The first and most fundamental is through the strengthening of local institutions so that they themselves may produce graduates with the best training possible under existing circumstances. A second method is through training within technical aid programs of graduates of local institutions. This overlays the academic experience of such young nationals with experience in the practical application of technical knowledge to the problems of the country involved. This process tends to sharpen the thinking of these young scientists and focus their attention upon those urgent problems of their own countries which they themselves can help to solve. It enables them to establish objectives and goals in their own minds so that if later they are given training abroad, they embark upon such a training period with a better knowledge of how to utilize this experience and how to apply it after returning to their own countries. A third training technique is the use of external fellowships or scholarships for the training of young nationals abroad, and an essential fourth technique involves the strategic utilization of their services after their return from a foreign experience.

The strengthening of local institutions may require operations at various levels. Frequently a major problem is the flow of farm youth to appropriate agricultural institutions and their ultimate utilization in the service of national agriculture. In such situations a first approach may necessarily be through the strengthening of vocational schools of agriculture and farm youth organizations. Coincidentally, superior schools of agriculture and agricultural research and extension agencies should receive support. This may involve aid leading to the improvement of staff, equipment, instrumentation, libraries, and curricula. The greatest single resource which any country can have is its youth, and their preparation for future responsibilities is of paramount importance in technical aid programs.

Often the most immediate need of an underdeveloped country is for the application of known and easily applied techniques for greater crop yields. Under such conditions concentration on farm management and agricultural extension pay great dividends. If at the same time the local institutions of agricultural education are strengthened, new methods, material, and personnel will begin to flow out and into the service of agricultural production. At this point it is possible to begin to take advantage of foreign training centers for the further development of those persons who may later become leaders in agricultural science for their own countries.

The in-service training of local scientists in operating programs is an invaluable method of training such personnel. If from the outset local scientists are associated with research and development projects, they gain great benefits from the actual participation and the association with specialists from abroad. It is through this type of activity that it becomes possible to select individuals for local responsibilities and others for further training abroad. Moreover, the number of persons receiving in-service training and growing into positions of responsibility is of greatest significance to the continuity and future success of technical aid programs.

The common and easy technique of foreign fellowships is one which can be badly abused, especially if the responsible agency makes the mistake of thinking that the award of fellowships and management of a fellowship system is an easy or simple task. The concept that the solution of all scientific problems is to select a number of individuals from underdeveloped countries and ship them abroad for advanced training is not necessarily a sound one. The abrupt transfer from an underdeveloped country to a large, modern, foreign university; inadequate program planning; the lack of the attention and understanding which a foreign student needs while in a country not his own—all may contribute to his confusion, discouragement, frustration, and in some cases even active resentment. The idea that all students who are trained abroad immediately become enthusiastic supporters of the way of life of the foreign country is an erroneous one, and there is considerable evidence that improper selection and handling of such students often does more harm than good. Too often fellowships are awarded on a quota rather than quality basis, and a few carefully selected, competent fellows are many times as valuable as a large number of poorly selected ones who perhaps through no fault of their own are in no wise ready to take advantage of such an experience. Moreover, the indiscriminate awarding of fellowships without any plans for the utilization of these young men after their return to their own countries is a grievous error which can only lead to future disappointment and discouragement and often active discontentment. Rather than establish fellowship programs of this nature, it would be much better to use the same funds to strengthen local institutions which are set in local traditions and which cater to local problems.

Obviously the majority of fellows from underdeveloped areas come to the United States for postgraduate training. In many instances this has been both a useful and satisfying experience for the trainees, but not in all. Too often fellows are poorly prepared on arrival and are disheartened by their failure to make a satisfactory record. Others are overwhelmed by instrumentation, with the result that on returning home they immediately demand tracer labs, ultracentrifuges, electron microscopes, and similar equipment as preliminaries to the establishment of local research projects.

It is not in the least suggested that the technique of fellowships be abandoned. On the contrary, this is a most important and significant way of supporting foreign technical aid programs and assuring their ultimate success. However, the same careful planning should go into a foreign fellowship program that enters into a technical aid arrangement. Carefully selected young men should be sent to institutions selected with equal care, and they should go with specific assignments, with the understanding that they will have definite responsibilities and career opportunities in their own countries upon their return. These young men can subsequently make real contributions to the solution of agricultural problems of their own countries, create opportunities for others, and generally improve the tone of science and education in the countries that they represent.

American institutions can be of invaluable assistance to underdeveloped areas through consistent efforts to provide the type of training most needed by foreign fellows. This requires some international understanding and some flexibility in the realization that the needs of foreign students are not necessarily identical with those of United States nationals. The sister-to-sister relationship between certain United

States land-grant colleges and their foreign counterparts has been a pioneer step in this direction and can have results of great benefit in the area of training in agriculture as well as in international understanding. It may well be that interested institutions should attempt to familiarize themselves with the needs of their foreign student guests, plan curricula with special reference to their needs, and award special recognition for their accomplishments. It does not seem logical that all foreign students should be forced into educational patterns and regulations precisely the same as those designed for national requirements.

The more effective training projects are those directed towards specific objectives. Thus it is much better to train scientists, locally or through fellowships for study abroad, for specific subsequent responsibilities. One of the great contributions which a foreign technical aid program can render is in this area. Aid to the establishment of nationals in positions of usefulness in agricultural education, extension, and research is of maximum future benefit. And this alone is not enough; it is often necessary to continue to aid these young scientists both morally and materially to become established and to direct or carry out projects and programs of significance to the progress of local agriculture as well as to aid in the training of subsequent generations of agricultural scientists.

II. Agricultural Collaboration in Mexico

The operating agricultural program of The Rockefeller Foundation had its beginnings in a request for technical assistance from the Government of Mexico in 1941. Prior to this time the Foundation had limited its operating activities to the field of public health. However, there was strong interest in problems of food production and therefore willingness to explore the possibility of being of assistance in this area through an operating program. As a result a committee of distinguished agricultural scientists was sent to Mexico in 1942. This group spent several months in travel and study, after which a report was made recommending the establishment of an operating agricultural program as the best method of helping Mexico to progress toward the satisfaction of its own agricultural requirements.

In 1943 an agreement was signed with the Government of Mexico, and the leader of the local project was sent to Mexico to organize the effort and get the work under way. The first move was a broad survey of agricultural conditions and potentialities in all of the different geographical areas of the country as well as visits to the several agricultural colleges and vocational schools, experiment stations, and farms of every description. During this period frequent conversations were held with farmers, students, teachers, scientists, administrators, and political leaders.

After several months it became apparent that greatest needs were for more corn, wheat, and beans, and that other important food crops were also in short supply. It also became evident that local crop varieties were inadequate, that soil fertility and management problems were serious and pressing, and that there were great annual losses due to the attacks of pests and diseases. From these facts it was decided to organize a program consisting of related projects in the fields of plant breeding, soils science, plant pathology, and entomology, and a search for staff was begun.

Since it was believed that staff represented the critical factor in the success of the entire program, the selection of staff members was accomplished slowly and carefully. Large numbers of universities and colleges and experiment stations were visited, and many outstanding young scientists were investigated as to training, experience, personality, and other pertinent qualities. In each case it was considered necessary to review more than just the qualifications of the candidate himself, since the abrupt change to a different country with importantly different traditions, language, and cultural patterns requires rather special types of abilities on the part of the entire family concerned. Dissatisfaction with aspects of life abroad on the part of either partner in a family has more serious implications than it might have at home, and it was recognized that responsibility for success or failure falls equally on both. This practice of extensive travel and investigation prior to the selection of staff, plus a visit to the foreign country by the candidate as a preliminary to a final decision, has paid definite dividends. At times it has seemed slow, but in terms of ultimate gain this has been unimportant. Both for the sake of the program and the individuals concerned, every effort has been made to avoid mistakes in the appointments of staff, and results have more than justified the time, care, and expense involved.

During 1943 and 1944 four staff members were appointed, and projects in corn, wheat, and bean improvement were initiated. They involved plant breeding, soils management and fertility studies relating to these three crops, and the investigation of those pests and diseases of major importance in limiting their production. In 1944 the co-operative program was organized as a special office of the Mexican Ministry of Agriculture, and the first young Mexican agricultural scientists were commissioned to the office for in-service training. From the beginning it was the policy of the group to minimize departmentalization in favor of a concentrated attack on important problems. This attitude has continued to prevail, and each scientist feels himself an important part of a total effort rather than the proprietor of a small area of one discipline.

From the outset it was recognized that efforts towards agricultural improvement in Mexico would have to be made in terms of the local medium. Not only were the climate, soil, pests, and diseases important, but available equipment, transport and storage facilities, and economic conditions were all of great significance. Prevailing customs and traditions had also to be taken into account, and it was therefore necessary to tailor materials and methods in such a way as to make them most useful and acceptable under local conditions.

Since corn has long been the primary food crop for the majority of Mexico's people, initial emphasis was placed on the improvement of this crop. Accordingly collections were made of corn varieties from representative areas throughout Mexico, from the United States, and from Central and South America. These were carefully tested in the several important corn areas in Mexico, and the most promising material was selected for use in the improvement project. As might be expected, it was not possible to introduce improved varieties from the United States corn belt for commercial production in Mexico. The best genetic materials from which to develop improved varieties for conditions in Mexico were found in Mexico, Guatemala, and other areas with similar climatic and physiographic conditions.

As the immediate need was for more corn, selections were made of the best material among the collections, and the most outstanding were increased for distribution. These open-pollinated varieties both contributed to increased production and helped to convince farmers of the value of improved seed. At the same time projects for the development of synthetic and hybrid varieties were initiated. As the synthetic varieties became available, they began to replace the various open-pollinated varieties and to set the stage for the acceptance of hybrids (Fig. 1).

By 1946 the significance of the improved corn varieties had become generally apparent, and in this year the Government of Mexico established a National Corn Commission, to increase, distribute, and promote the use of improved varieties. Thus when the first hybrids became available, there was an agency prepared to undertake their increase and distribution to interested farmers. However, it was recognized that no attempt should be made to convert all of Mexico to the production of hybrid varieties or to produce hybrids exactly similar to those used in the United States corn belt. Open-pollinated varieties are still of importance in many areas, as are the multiple top crosses or synthetics.

Moreover, it was not practical to attempt to use hybrids produced from late-generation inbreds under Mexican conditions. It was therefore decided to develop hybrids from early-generation inbreds in order to retain a degree of rusticity as well as stability. This has proved practical and has in effect created a special pattern for the production of improved varieties of corn for areas with special conditions such as those which exist in Mexico. Currently nearly a fourth of Mexico's corn acreage is planted to improved varieties with average increases in yield of from 25 to 30 per cent.

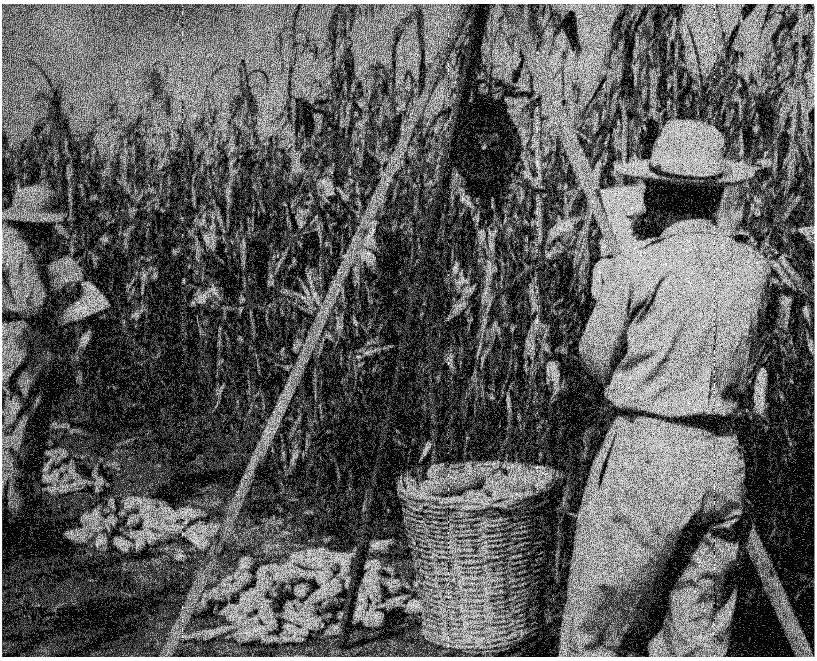

FIG. 1. Yield trials of improved corn varieties—Morelos, Mexico.

Wheat improvement proved to be as fascinating a task as the improvement of corn. The so-called native varieties of wheat grown in Mexico were found to be well adapted to local growing conditions but of fair to poor quality and completely susceptible to established races of black stem rust. In fact, wheat was traditionally grown under irrigation in the dry season because of the impracticality of trying to produce this cereal under conditions favorable for the development of stem rust. Previous efforts to introduce high-quality rust-resistant

United States and Canadian wheats to combat the wheat rust problem had not proved effective, as they were not well adapted to growing conditions in Mexico.

Again collections of varieties from important wheat-producing areas were made, and these now numbered in the thousands. Since, unlike corn, wheat is not indigenous to Mexico, it was necessary to draw genetic material from widely varying sources throughout the world. These in combination with native varieties resulted in the production of high-quality rust-resistant varieties adapted to conditions in Mexico. Over the years materials from such widely separated areas as Texas, Minnesota, Canada, Italy, Peru, Africa, Australia, and Egypt have been utilized in the formation of improved varieties for the several important wheat-producing areas of Mexico. Currently over 75 per cent of the Mexican wheat crop is derived from them, and wheat may now be grown during the rainy season with attendant economic advantages. Yields from the improved varieties range from 30 to over 50 per cent more than the yields of those which they replaced.

The introduction of Race 15B of stem rust into Mexico in 1949 was a severe blow to the wheat improvement program, but fortunately resistant material was already available, and the new varieties which have been released subsequently carry resistance to this race as well as to the other major races found in the country. They are increased and distributed by a Wheat Commission, established within the Ministry of Agriculture. This organization greatly facilitates the rapid dissemination of new varieties, and the commission now handles several thousands of tons of seed wheat each year.

Beans are an important item of diet in Mexico and are widely grown. However, yields are low owing to poor stands and losses due to the attacks of pests and diseases. Quality is variable from very good to poor, and local preferences are strong. Accordingly no attempt was made to substitute varieties, but rather to improve the yields of those commonly grown and widely accepted. Major problems proved to be seedbed preparation, soil infertility, anthracnose, root rot, virus diseases, bean beetles, and the bean pod borer. These were all given attention along with a project to produce healthy, uniform seed of selected varieties. Collaterally a breeding program was initiated for the production of improved varieties for future introduction.

From the first it was clearly recognized that soil improvement was fundamental to any progress which might be made in increasing the production of Mexico's three major crops. Therefore, a broad program of soils research was initiated with the beginning of the collaboration, and this has been a major factor in all subsequent developments. The work in soils has been concerned with land preparation, rotations, the use of green manure crops, field crop introduction and testing, and the investigation of fertilizer requirements (Fig. 2). The great benefits which accrue from rational soils management practices are readily demonstrable, and these practices have increased markedly since the establishment of the first demonstration in 1944.

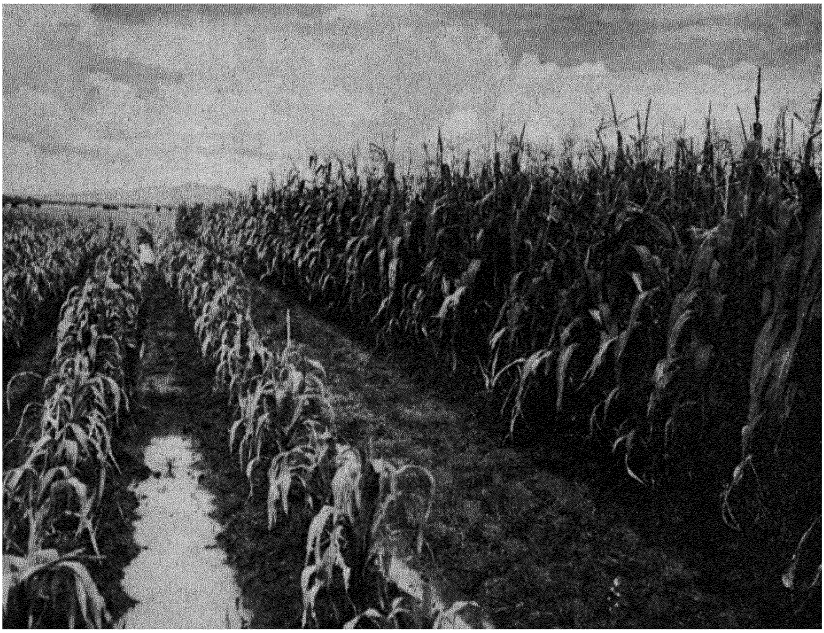

FIG. 2. Fertilizer experiments on corn—Rocamex Experiment Station, Irapuato, Mexico.

The foregoing paragraphs are intended to illustrate the early technical phases of the collaboration in Mexico. At the same time other developments were also taking place. The small experiment station established on land of the National College of Agriculture in 1944 grew to one of approximately 300 acres and became a land-grant college type of agricultural experiment station. A field station building and greenhouse were constructed, and farm and laboratory equipment was increased as needs required. Other stations were added in strategic areas, and projects were established at already existing Federal or State stations. Large numbers of demonstration plots were established with farmers in many areas, and the program began to extend into the tropics. Field days for farmers were held regularly with steadily increasing attendance, and farmers' and technical bulletins were issued describing the results of research projects.

In the training phases of the program, the number of Mexican commissioned personnel increased rapidly, and some of the first appointees left the office for positions in government or for postgraduate training through scholarships granted by the office. They were replaced by recent graduates of the local agricultural colleges, many of whom had worked at the experiment station during vacation periods. As the numbers of staff and commissioned personnel increased, the program began to extend geographically, so that by 1948 work was in progress in twelve of Mexico's twenty-eight states. Laboratories had been expanded and improved and a research library established, and many scientists from other countries had begun to visit the project in Mexico. Some of these came as observers and others as trainees, who after one or more years with the program in Mexico returned to their own countries to engage in agricultural research.

Once the possibilities for the improvement of the three principal food crops of Mexico had been demonstrated, other opportunities presented themselves. One of the first was the necessity for a grain crop to replace corn in those areas where rainfall is insufficient for normal corn production. This need was responsible for the addition of a sorghum project (Fig. 3), and various types are now planted to thousands of acres in Mexico each year. Forage legumes, grasses, and soybeans were added to the crops included in the research program, the former in support of animal industry in Mexico. More recently a vegetable improvement program has been started, involving potatoes on the one hand and truck crops on the other. As a result Mexico's potato yields and total production are increasing, and certified potato seed produced in Mexico is becoming available. The vegetable project involving tomatoes, onions, crucifers, cucurbits, and other table vegetables has resulted in the development of a number of superior varieties adapted to Mexico and the production of some seed for local use.

In all of these efforts the attack has been on a team basis. The entomologists have worked with insect pests of corn, wheat, beans, potatoes, and vegetables; the pathologists have worked with rusts, smuts, root rots, viruses, blights, and wilts attacking the several crops; and the soils scientists have studied the nutrient requirements of each crop in terms of major elements, time and placement of fertilizers, and other factors. In the meantime the plant breeders have continued to improve genetic stocks. This work has not all been purely practical; on the contrary, considerable fundamental research has been continuously in progress. Results include: specially designed breeding techniques for corn and wheat to meet the needs of areas like Mexico; a study of the indigenous races of corn in Mexico; investigations of the transmission of virus diseases of corn; the role of clay minerals in Mexican soils; and investigation of the physiologic races of the fungi causing stem rust of wheat and late blight of potatoes.

FIG. 3. Sorghum selection and improvement—Irapuato, Mexico.

As the research program developed, a growing need for agricultural extension was recognized. As there was no extension service in Mexico, efforts were made to get this type of activity under way through demonstrations and field days, but initial progress was slow. In 1950 it became possible to work with the officials of one state in the establishment of a testing, demonstration, seed production, and extension program. This developed rapidly and gained wide acceptance in the state, other states expressed interest in similar projects, and several began smaller programs. In 1953 the Federal Government of Mexico initiated an emergency extension service to aid in increasing production of the basic food crops, and it is planned to convert this effort into a national extension service in 1954. This should result in a more rapid transfer of the results of research to increased food production. Initial emphasis has been placed on corn, beans, and wheat, but other crops are to be added in the future. A large proportion of the young Mexican agronomists who are carrying on the actual extension activities have had previous training and experience in the co-operative program herein described (Fig. 4).

FIG. 4. Mexican agronomist explains wheat improvement program to farmers—El Mexe Experiment Station, Hidalgo, Mexico.

By 1950 the collaboration in Mexico had become quite international in scope. Staff members regularly participated in international meetings in the United States and visited numerous other countries in Latin America, and many Latin American and United States scientists had visited or studied in association with the program. Seed and other plant materials, as well as the numerous publications on results of research, were widely distributed in response to requests. Two international meetings of Latin American agricultural scientists had been sponsored. In the same year it was decided that in response to an official request the work would be extended to Colombia through the establishment of an operating program in that country.

In the succeeding years a number of additional international activities were initiated, and those already mentioned continued. They included co-operation with the United States Department of Agriculture, first, in testing the world wheat collection for resistance to races of stem and other rusts in Mexico, Colombia, and Peru, and second, in testing the world barley collection in Mexico and Colombia. Co-operation was begun with appropriate centers in the establishment of a Latin American testing project involving study of resistance of potatoes to races of late blight existing in several countries. The programs in Mexico and Colombia both began collaboration with the National Research Council of the United States in the establishment of maize germplasm banks in those two countries. International meetings were fostered, among them one of plant scientists meeting in Brazil, one of soils scientists in Mexico City, and a third of agricultural librarians from Central and South America meeting at Turrialba, Costa Rica.

Two types of scientific aides receive appointment to the efforts in Mexico and/or Colombia, one, the "Temporary Scientific Aides," consisting of postgraduate North American students interested in Latin American agriculture, who are sent for a year's experience in association with the programs, and the other, the "Special Temporary Scientific Aides," being distinguished North American agricultural scientists who would contribute to research in progress and obtain some familiarity with Latin American agriculture and research and educational institutions. And to the present, a total of forty-nine young agricultural scientists from Central and South America have received training and experience in the Mexican Agricultural Program.

Most recently inquiries have been received from several countries in Central America regarding the possibility of some assistance in improvement of basic food crops, principally corn, in that area. These inquiries were stimulated by several facts, among them that a number of young Central American agricultural scientists had received training in the Mexican Agricultural Program and subsequently had tried improved seed from both Mexico and Colombia in their own countries. Several varieties proved superior to local ones, and not only has the area under cultivation to the new ones been increased, but interest has been created in a more active program of food crop research. Accordingly it has been decided that a small project for the testing of improved corn varieties in several parts of Central America will be begun in 1954 with Rockefeller Foundation assistance, there being the possibility that it may develop into a program which will provide superior and adapted seed of corn and possibly other food crops to the farmers of the several interested countries.

The current situation with reference to the program in Mexico is quite different from that of eleven years ago. During this period approximately 220 young Mexican scientists have received training and experience in the co-operative program. Between forty and fifty of these have held Rockefeller Foundation scholarships for postgraduate study in the United States, and three have had foreign experience in Costa Rica, Colombia, and Brazil, respectively. These past trainees are now scattered throughout Mexico, many in the national extension service; a number have become professors in the several Mexican colleges of agriculture; others are directing local experiment stations or specific research projects; still others are engaged in state agricultural programs; and several are employed by the national agricultural banks. A few have gone into commercial enterprise with canneries, agricultural machinery companies, insecticide and fungicide corporations, and cotton and tobacco producing companies; and a few have entered the field of agricultural production on a private enterprise basis.

The scholarship program for Mexican agricultural scientists has been most productive, and scholars have studied at agricultural institutions in Massachusetts, Pennsylvania, New York, Ohio, Michigan, Wisconsin, Minnesota, Kansas, Texas, Colorado, Iowa, North Carolina, and California, in accord with their special needs. Each scholar has been carefully selected, as has the institution chosen for his training. In addition every effort has been made to place these scholars under the supervision of leading agricultural scientists who have had some experience in Latin America. In a number of instances experience in Latin America has been provided for United States faculty members with a special interest in the training of foreign students. During their study period in the United States the scholars have each been visited by a Foundation staff member, who investigated the scholar's program and social adjustment. At the termination of the training period the scholars are returned to Mexico, frequently by an indirect route to enable them to visit important agricultural centers, and upon their arrival in Mexico each has been placed in a previously agreed-upon position of responsibility commensurate with his training and experience. In a few instances these young men have returned to the United States at a later date, have successfully completed the requirements for the Ph.D. degree, and are again in Mexico rendering valuable service in agriculture. Six of the forty-odd returned scholars now have official status as regular staff members in the agricultural program carried on co-operatively by the Mexican Government and The Rockefeller Foundation, and others will be added to the staff as rapidly as they qualify.

Research projects of various types have now been established in all of the important agricultural areas of Mexico. Work with corn is in progress in the principal corn-producing areas ranging from elevations of over 9000 feet to sea level and from temperate climate to both the tropics and subtropics. The wheat improvement program is largely concentrated in two areas, namely, the Bajio of the central plateau and northwestern Mexico, although there is a third center in the north central part of the country. Bean improvement is being carried on throughout the central plateau and extends into the Valley of Mexico and the subtropics. Similarly work with other crops is located where they are most important or are best adapted. Projects in force are being carried out principally as part of the over-all agricultural program of the Mexican Ministry of Agriculture, but collaboration has also been afforded to state governments in Mexico engaged in state agricultural programs.

The benefits of research are being rapidly extended to all interested farmers through the efforts of the National Extension Service and the Wheat and Corn Commissions, which are entities within the general structure of the Ministry of Agriculture. Great progress has been made in the annual increase in the quantity of improved seed available and in its effective distribution for maximum production. A modern seed-handling plant has been constructed by the Corn Commission in the state of Celaya and is rendering effective service to corn producers in that area. The use of fertilizer has increased enormously, especially since the completion of an ammonium sulfate plant constructed by the National Government. The increased use of both nitrogen and phosphate fertilizers has resulted in larger yields and in greater and sustained demand for more fertilizers. The use of green manure crops has increased, and various types of legumes are now planted in rotations or in association with food crops such as wheat and corn. The application of insecticides and fungicides for better crop yields has become more common in Mexico, and as further information is made available, it is expected that their use will increase. Among the food crops, beans and potatoes account for much of the consumption of these materials (Fig. 5). The use of herbicides, unknown in Mexico several years ago, is gaining in importance, and they are now used for the control of weeds in large acreages of wheat and to a lesser extent in corn. New uses are developing rapidly, involving such crops as rice and sugar cane.

The importance of agricultural education in Mexico has not been overlooked. Not only has the co-operative program developed new faculty for the principal agricultural schools, but a number of the more mature faculty members have been given opportunities for postgraduate study. Additional support has been provided in the form of research grants and grants for laboratory equipment and library materials. Promising undergraduates have received part-time employment. As a result of these activities the research output of the schools has increased, and one or two are now extending their services to farmers through the establishment of short courses.

The role which Mexican Government officials and Mexican scientists have played in the entire development described herein is a major one. Not only has the Ministry of Agriculture over the years provided land, labor, the salaries of commissioned personnel, as well as contributions to construction, but it has also contributed direct subsidies to the operating activities. A major proportion of results obtained to date are directly due to the efficient and dedicated services of the commissioned personnel. These Mexican agricultural scientists associated with the program have demonstrated fine qualities of industry, enthusiasm, and research ability. They have steadily accepted increased responsibility, and those who have moved from the office in Mexico to positions of greater importance have continued to contribute significantly to agricultural progress.

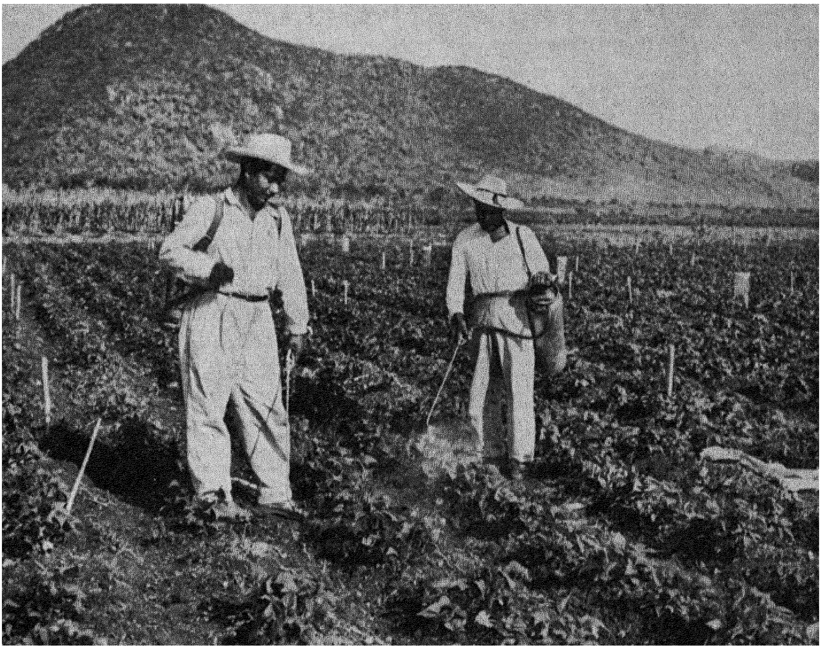

FIG. 5. Experimental control of bean insects—Jaloxtoc, Experiment Station, Morelos, Mexico.

III. Agricultural Collaboration in Colombia

The co-operative program in Colombia, although less than four years of age, has grown with great rapidity. Experience gained in Mexico, as well as improved plant materials from the Mexican program, enabled the staff in Colombia to make early progress. The first staff members sent to Colombia were transferred there from Mexico, which was also a great advantage.

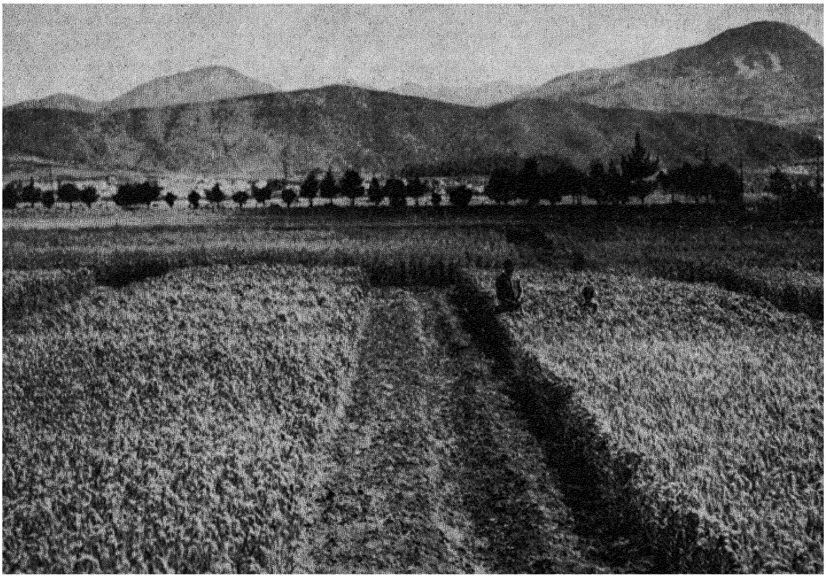

Fig. 6. Experimental plantings of wheat—Caldas Experimental Station, Bogota, Colombia.

As in Mexico, the program was organized as a special office of the Ministry of Agriculture with both Rockefeller Foundation and Colombian personnel joining forces in conducting the various research activities. As corn, potatoes, wheat, and beans are of major importance as food crops in Colombia, these were the subjects of the first research projects. And since there are three distinct climatic zones in the country, work was begun simultaneously in each (at Bogota, Medellin, and Palmira). Already the combined efforts of the Colombian and North American scientists have resulted in evident improvements in corn and wheat varieties (Fig. 6), and these form the basis of a Government seed increase and distribution program. Progress has been made in the control of potato disease, and much is being learned of the problems of bean production in Colombia, some of which are being overcome.

Recently additional projects involving grasses and legumes, barley, and green manure crops have been established, and these are also being approached from the standpoints of breeding for varietal improvement, soils management, and disease and pest control. Approximately forty Colombian and eight United States scientists are involved in the entire research program, and the first scholarship candidates are being selected for postgraduate training.

In Colombia as in Mexico the agricultural effort has been a truly co-operative one. The Colombian Government has provided a wide range of important facilities which have aided programs to date, has commissioned a considerable number of young Colombian agricultural scientists to the co-operation, and has directly subsidized the office during each year of its existence. The Colombian scientists associated with the office have worked intelligently and indefatigably toward the improvement of agricultural methods and materials leading to increased food production for all of Colombia's people. Their role in the entire operation is one of incalculable value.

IV. Summary Statement

It should perhaps be repeated here that the present article is intended to describe only one technical aid pattern. The programs dealt with here have now been in operation for a sufficient period of time to permit an estimate of accomplishments, which it is believed have been both numerous and beneficial with respect to the established objectives. It is in no wise implied either that there is only a single pattern for operations in agriculture or that the method described herein is applicable to all of those countries in which technical aid programs in agriculture might be undertaken. In fact, the programs in Mexico and Colombia differ in numerous respects in recognition of differences in local situations. It is believed, however, that results in Mexico and Colombia serve to establish certain useful principles and a pattern which may be helpful in similar efforts. A summary of the procedures which have proved effective follows:

1. Foreign technical aid programs should be established only after a clearly demonstrated interest and enthusiasm on the part of the recipient government and the individuals most directly concerned and after a thorough preliminary survey of agricultural potentialities, local personnel resources, and economic possibilities resulting in the conclusion that a useful operation can be initiated.

2. Staff members assigned to foreign technical aid programs should be selected with extreme care and chosen on the basis of qualities of leadership, character, and personality in addition to unquestioned attainment in their special fields of agricultural science. The qualities of the rest of the family for foreign service should also be taken into consideration. Finally, it is highly necessary that staff members be assured of the stability of the positions to which they are appointed and that the posts offer sufficient career opportunity to attract individuals of highest caliber.

3. In any agricultural improvement program it would seem desirable to begin with those problems which are of major significance to the population of the country concerned, and these should be selected in agreement with the appropriate persons in the country. It is believed that projects should be strategically located, started on a modest scale in an effort to minimize errors, and permitted to grow only as rapidly as accomplishment dictates. It seems only good sense not to make impressive initial announcements of what is going to be accomplished. If the actual accomplishments fall short of such predictions, then hard feelings and disappointment will result. If the actual accomplishments are impressive, then they will speak for themselves.

4. In the establishment and subsequent development of local projects every effort should be made to utilize qualified local personnel, either directly as partners in the enterprise or as trainees when younger and less experienced individuals are concerned. They should have opportunity to participate in every phase of a program and to acquire increasing responsibilities as their experience broadens and as they demonstrate capacity to accept such responsibilities. As rapidly as possible local personnel should be inserted into key positions which provide career opportunities.

5. Collaterally with any program involving research, extension, or education in agriculture, each of the other two should receive attention. In the last analysis a research program cannot rise higher than the level of the local personnel emanating from the agricultural colleges, and neither can it be more effective than the degree to which its results are transmitted in a useful fashion to agricultural producers.

6. Every attempt should be made to draw on other countries for methods and materials which may be useful to the program under consideration, and in addition such progress as is made which can be useful elsewhere should be made available freely to agricultural scientists in other countries. The exchange of personnel and information and the technique of small scientific meetings, bringing together the leading agricultural scientists of an area, contribute to the success of an operat-

ing program in technical agriculture. Regular publication of results in appropriate form is essential.

7. The ultimate objective of any program of foreign technical aid should be one of creating a situation in which the program is no longer necessary. It is a simple matter to state this as a goal, but in practice it is necessary that it be kept in mind always and that a continuous effort be made to reach it. This means that program planning must take into consideration the requirement that the projects established are the type which can be built into the scientific, economic, and social structure of the country in which they are located. Training programs should be directed to producing a large body of capable personnel for specific responsibilities leading towards the ultimate nationalization of the program in force.

It does not seem desirable or possible that a point may be reached at which abrupt total withdrawal should occur, but rather that this process be gradual and take place over a period of years when it is evident that it is feasible to initiate a withdrawal movement. Even after this has been totally accomplished, there may be opportunities to provide special types of support for a period of several years to enable the projects to continue as planned. Subsequently these should be self-propelling, self-expanding, and measurable in terms of increased agricultural production and progress. At this point the co-operating agency will be in a position to know that its efforts have been successful and that a real contribution to the agricultural evolution of the country in question has been made.

With reference to the co-operative program in Mexico the Foundation is looking ahead toward the time when it will be both possible and constructive to replace gradually its North American staff with equally competent nationals. This in no wise implies lessened opportunities for the North American staff members, who become more valuable to The Rockefeller Foundation each year and more in demand in the field of international agriculture. No date is set for this proceeding, but rather it will take place as qualified personnel become available, are appointed by the Government to appropriate positions of responsibility, and begin to provide the necessary leadership. Simultaneously with this movement The Rockefeller Foundation's emphasis will be shifted to supporting the activities and preparation of the local scientists as an aid to the eventual complete assimilation of the program by local agencies. It is believed that if this can be accomplished, the fundamental aims of technical assistance will have been attained.

New Concepts of Management of Corn Belt Soils

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I. INTRODUCTION

The art of farming has seen many changes since the beginning of civilization. Tractor power on the farm is replacing animal power, which, in turn, has been replacing much hand labor, or man power. But man power has also been reduced through the introduction of types of machinery and equipment to which the greater power of the animal and the tractor could be harnessed. Among such implements, the plow and the row seeder may be acknowledged as leaders responsible for great changes in the art of farming, for they introduced the row crop into farm management. More recently the introduction of power machinery on a large scale has brought significant changes in farm management practices. Today, in the central United States, the cultural practices for row-crop production, especially corn, are undergoing a re-examination. Many of the new experimental cultural practices being tested are based on old ideas which in the past were unsuccessful but which now, through new knowledge, are being shown to be practical.

The science of farming has, in recent years, advanced much faster than the art of farming. Present-day technical knowledge of soil management and fertilizer usage is far ahead of practical adoption, or actual use. Many of the practical applications of the scientific knowledge of farming are not being adopted, or are being delayed in acceptance, because they require a change in the art of farming. Unlike the science of farming, the art of farming is handed down from one generation to the next, with the result that many farmers are reluctant to discard operations which have proved successful under past concepts. Almost all advances in the science of farming have involved changes in methods of operation and the substitution of capital for labor. Therefore, advances in the scientific knowledge of farming sometimes have been only partially brought before the farmers by extension or advisory workers, because acceptance often involved scarce or expensive equipment and materials calling for capital outlays. It is the purpose of this paper to examine some of the objectives underlying the new tillage and cultural practices being tested for cultivated crops in the Midwest, and to evaluate some of the concepts on which the objectives are based.

II. The Old Practices

The most common tillage implements on a farm are the plow, the disk, the harrow, and the cultivator. All of these have two things in common: they stir and aerate the soil, and they are used in the control of weeds. Then there are many types of special tillage implements such as listers, subsoilers, rototillers, and rollers, which have specialized uses or which accomplish a specific effect for special soil conditions.

The moldboard plow, or its counterpart of ancient times, probably always has been the implement most commonly used to stir or turn the soil. It is used to:

1. Loosen the soil.
2. Turn under surface residues.
3. Destroy weeds.
4. Prepare a seedbed or promote a favorable soil structure.

The disks, harrows, and cultivators (both field and row) are tools used for:

1. The control of weeds.
2. The conservation of moisture both through decreased evaporation from the surface and increased penetration of rainfall.
3. The partial covering or burying of residues.
4. The formation of a favorable soil structure, or tilth.

That these tools helped in the accomplishment of many of these objectives in the past is obvious from their long and consistent use on all types of farms. These objectives were based on the concepts that tillage and more tillage, clean cultivations, and absence of all cover were good for the soil. Experimentally, when applied to virgin soils high in organic matter, these concepts appeared to be valid, for increased yields could always be recorded for a tillage operation.

In farming, as in many other endeavors, it is not always possible to evaluate the success of an operation by the exactness with which it appears to meet its obvious objectives. This has been true of farm tillage operations. Most research workers would agree, perhaps, that excessive, or even moderate, tillage of the soil has been a decisive factor in the destruction of soil organic matter. As the soil was stirred and aerated and soil organic matter oxidized, the nitrogen released during the accelerated decomposition of soil organic matter was reflected in a yield increase for the tillage operation. Literally hundreds of references prior to 1945 could be cited to show that one tillage operation or the other, as compared to nontillage, resulted in an increased crop yield. Although immediate objectives have been attained by tillage, it has proved harmful to many soils. Among the more important and obvious harmful results of excessive tillage have been:

1. Rapid loss of soil organic matter and loss of soil tilth.
2. Excessive soil erosion resulting from lack of cover under clean cultivation, and the too-fine breakdown of the soil structure.
3. Increased loss of water due to excessive evaporation from the bare surface, and poor penetration of rain water where desirable soil structure has been destroyed.

Among the various cultivated crops for which tillage operations are performed, the deleterious effects of tillage are most pronounced on the row crops. For many years corn, soybeans, and cotton have been identified as the worst soil-destroying crops a farmer could produce. The erosion havoc in the corn and cotton belts is all too obvious to need comment. Much of this damage was brought about by overtillage in an attempt to gain the last drop of nitrogen from decomposing organic matter, for few crops have higher fertility requirements than do the row crops. At the same time, it must be recognized that the row crops are among the highest income-producing crops, so the farmer can be expected to continue their production. It becomes essential, then, to re-evaluate tillage and management practices for these crops, and to attempt to devise methods of tillage and management that will lessen the harmful effects resulting from their production. Critical analysis of row-crop production will show that it was the management and tillage practices imposed on these crops that were responsible for soil deterioration, not the crop itself. Briefly stated, overtillage and underfertilization, especially with nitrogen, were responsible for much of the soil damage. The problem is not to show that cultivation of row crops growing on soils the organic matter of which has been depleted, causing them to cake or crust badly, will result in increased yields of a crop, but rather to determine how such soils should be handled so that they will not cake or crust in the first place. The question is this: how should cultivated crops, especially the row crops, be tilled and managed so that they will become soil conserving? The solution to this question is the primary objective of experiments with the newer tillage implements and fertilizer practices being carried on in the Midwest, with management practices revolving around the concept of high nitrogen use, unattainable through legume rotations alone.

III. The Bases for the New Concepts and Practices

In the last few years many suggested cultural practices and many new tillage implements have been introduced on an experimental basis to overcome some of the obvious objections to clean-tillage practices. Among these cultural practices are mulch systems, both trash and living mulches, sod seedbeds, plowless farming, silt farming, and many others. Almost all of these cultural practices are being investigated with one or more of the following objectives in view:

1. Erosion control—to be achieved through minimum cultivation, adequate fertilizer use, and a mulch cover for the land.
2. Organic matter maintenance or build-up—to be achieved through adequate nitrogen use, extra residues from living-mulch growth, and minimum cultivation of the land.
3. Weed control—to be achieved through mulch covers, minimum cultivation, and chemical sprays.
4. Optimum soil tilth—to be achieved through high fertility, minimum cultivation, living and trash mulches, and an adequate supply of active soil organic matter at all times.

Many of these objectives are associated with special types of equipment, among which are the mulch planters, ridge seeders, subtillers, and trash cultivators. These all have one characteristic in common, that of leaving the surface of the soil rough, covered, and as undisturbed as possible, but their success is tied in with a management program calling for a positive nitrogen balance for the soil.

At this point it should be noted that these objectives are not too different from those listed for the plow and cultivator. What is the basis, then, for thinking that these new cultural practices and their associated implements will be of more value in the accomplishment of these objectives than the old equipment and management practices now in use? The answer lies in new scientific knowledge revolving around the use of nitrogen, which at the moment may be considered tentative but which, in its preliminary stages, seems very encouraging for the fulfillment of the stated objectives.

1. Effects of Commercial Nitrogen on Soil Management

Nitrogen fertilizers became available to the farmer at the close of World War II in quantities large enough to compete with legume nitrogen. Since 1950 the corn-belt farmer has been able to choose whether to grow or buy his nitrogen. Nitrogen fertilizers opened the way for new management practices where erosion was not a serious problem. Legumes which were included in rotations to supply nitrogen to the nonlegume crops are not now necessary for that purpose. With the favorable economic position that corn has enjoyed since the war, many farmers have increased the frequency with which this crop has appeared in their rotations (with others going all the way to continuous corn), with a corresponding decrease in legumes and increase in fertilizer nitrogen. Contrary to the expectations of many investigators, the substitution of commercial nitrogen for the legume in the rotation has not been disastrous. On the contrary, it has focused attention on the limitations of many management practices formerly considered sound and desirable. Similarly, nitrogen may also have given the newer cultural practices an unjustified acclaim, with yield increases due to adequate fertilization being confused with, and ascribed to, the new tillage practices.

TABLE I

Morrow Plots. Effect of Rotations on Nitrogen Content of the Soil

Rotation	Plot	Treatment	Nitrogen content of soil, lb./acre 1904	1943	Loss	Average corn yields,* bu./acre
Continuous corn	3 NE	None	3840	2700	1140	25
Corn–oats	4 NE	None	4290	3380	910	34
Corn–oats–legume	5 NE	None	5230	4040	1190	53

* Average yields, 1904 to 1952, for years when all plots were in corn.

A study of crop rotation experiments of the past shows readily that the "good" rotation was usually the one that contained legumes most frequently, with more nitrogen thus being supplied to the nonlegume crops. The success of the rotation was usually measured by the yield of the cash crop that immediately followed the legume. This meant, then, that the more and better the legume growth, the better the rotation. But the use of yield alone for evaluating a rotation can be very misleading. Some unpublished data from the Morrow plots at the University of Illinois (Table I) help to illustrate how a rotation may show a yield increase for a cash crop and still be doing considerable harm to the soil. The corn-oats-legume rotation on these plots, where no residues were returned, has been producing much higher yields than the corn-oats or the continuous-corn rotations, but as far as the loss of soil nitrogen, and hence soil organic matter, is concerned, the corn-oats-legume rotation has been as "hard" on the soil as the continuous-corn rotation. If the legume residues had been returned, the rotations would have shown considerable difference in the amounts of nitrogen lost. What the data do indicate, however, is that if the legume residues are removed, which is essentially what happens when a legume failure occurs, so that no nitrogen is returned to the soil, the depletive action of all rotations for soil nitrogen is similar. In other words, rotation studies in the past were often essentially nitrogen studies, with crops having the highest nitrogen requirement causing the greatest, or most rapid, loss of soil nitrogen and, consequently, soil organic matter. Today, with commercial nitrogen available to add to the nonlegume rotations, many of the poorer rotations of the past, when supplemented with nitrogen, may prove to be better than our present good legume rotations.

As more commercial nitrogen has become available, several short-time experiments have shown that continuous corn grown on relatively flat land has not caused a measurable decrease in soil organic matter when adequate nitrogen has been supplied. In a five-year study, Breland (1952) found that a slight increase in soil organic matter occurred when continuous corn was provided with adequate nitrogen and extra residues were returned to the soil. Unpublished data from other work done at Illinois have indicated that soil organic matter can be increased faster when minimum tillage is imposed upon the continuous-corn rotation. Most preliminary experiments seemed to indicate that adequate nitrogen alone was unable to maintain the level of soil organic matter under a continuous-corn rotation and conventional clean-cultivation management.

Miller (1951) has published some data from the Illinois Experiment Fields (Table II), which, when recalculated, show that on some of the best naturally fertile soils in Illinois, which generally have not responded to lime, phosphate, or potash treatments, only small amounts of nitrogen, 80 to 100 pounds per acre per rotation, were needed to give yield increases for corn almost equal to those obtained with a corn-corn-oats(legume catch)-wheat(legume catch) rotation. It should be noted that these data show a comparison between the use of nitrogen alone on plots that had previously been without treatment for many years and plots where the rotation and treatment had been established for a long time. These yield differences represent all of the benefits derived from long-continued use of legumes and the return of crop residues, after the 80 to 100 pounds of nitrogen have been subtracted. Since the nitrogen treatments were not started until 1943, whereas the check plots and RLPK treatments were started about 1910, no valid comparisons can be drawn from the organic-matter levels of these soils resulting from the use of nitrogen. The data, however, tend to support the concept that the beneficial action of the legume in a rotation, when erosion is not a serious problem, is due largely to its nitrogen.

TABLE II

Yield Comparisons of Legume and Synthetic Nitrogen

Field	Average corn yields, 1943-1950, bu./acre			
	Check*	Check + N	RLPK**	Increase for RLPK and legume over N alone
Minonk	51	67	72	5
McNabb	53	80	86	6
Hartsburg	57	71	77	6
Aledo	52	72	71	−1
Kewanee	48	58	62	4

* Check = No residues returned.
** R = Residues returned.
L = Limestone.
P = Rock phosphate.
K = Potash.
N = Nitrogen.

A study of soil organic matter in some Illinois soils by Lee and Bray (1949) showed that all rotations with only one standover legume crop in four years were depleting with respect to soil organic matter. Stated another way, the total nitrogen added by symbiotic fixation was less than that required by the nonlegume crops, and therefore soil nitrogen was being used at the expense of decomposing soil humus. The general relationship that exists between nitrogen additions and the loss of soil nitrogen is shown graphically in Fig. 1, based on data from Lee and Bray (1949). These data are admittedly incomplete, for the amounts of nitrogen added by the systems have not been adequate. All of these soils are capable of yielding more than 100 bushels of corn per acre, and even the best treatments lost soil nitrogen. But the data support the concept that the average yearly losses of soil nitrogen, and hence soil organic matter, decrease as high yields are obtained with increasing nitrogen use. Projection of the data (the dotted portion of the curves in Fig. 1) seems to indicate that if the amount of nitrogen used had been equal to or slightly more than crop removals, the soil losses could have been reduced to zero. Such data as these tend to support the concept that high yields cannot be obtained without adequate nitrogen fertilization, and that maintenance of high yields and adequate nitrogen use are compatible with the maintenance of good soil physical conditions and organic matter.

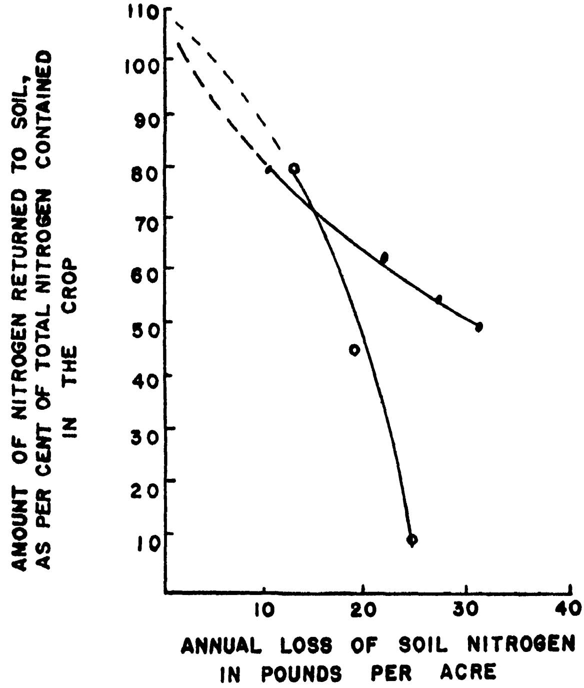

FIG. 1. Per cent of nitrogen in crop that is applied to soil in relation to nitrogen lost as soil organic matter. (●—Average values for 6 soils having over 4500 lb. per acre total nitrogen. ○—Average values for 4 soils having less than 2500 lb. per acre total nitrogen.)

Many experiments are now in progress to ascertain whether it is possible, or desirable, to build up soil organic matter by adding more nitrogen to the soil than is removed by the crop. Preliminary data indicate that build-up of soil organic matter can be done by using small excesses of nitrogen along with a legume program. Some unpublished data from the Brownstown Experiment Field in Illinois may be cited as an example (Table III). Here identical treatments, except for nitrogen, used in conjunction with a good legume rotation are compared. Both the organic-carbon and nitrogen contents of the soil are higher as a result of a small nitrogen application, an average of 30 pounds of nitrogen per acre per year, along with a legume program. However, this may represent only a slower rate of decrease for the nitrogen treatments as compared to the no-nitrogen.

TABLE III

Nitrogen and Carbon Gains in Soil with Nitrogen Treatment, 1940 to 1951

Brownstown Experiment Field—Illinois

Plot No.	Treatment*		Nitrogen, %	Carbon, %
415-C	NRLsPK		0.122	1.14
404-C	RLsPK		0.114	1.05
		Gain	0.008	0.09
305-A	NRLsPK		0.117	1.20
311-B	RLsPK		0.096	1.10
		Gain	0.021	0.10
107-B	NRLsPK		0.111	1.12
106-A	RLsPK		0.099	0.86
		Gain	0.012	0.26

* Rotation = Corn–soybeans–wheat–(legume–grass mix).
N = Nitrogen treated—30 pounds per acre.
R = Residues returned.
L = Limestone.
sP = Superphosphate.
K = Potash.

Unlimited experimental evidence is available to show the value of legumes as partial conservers of soil organic matter. Soil organic matter is usually thought of as a residual product of decomposable residues and microbial tissue. By analysis, organic matter usually contains about 5 per cent nitrogen, and 0.5 per cent each of phosphorus and sulfur. The ratio of carbon to nitrogen to phosphorus to sulfur is usually about 100 to 10 to 1 to 1 in extracted soil organic matter. With the increased supply of synthetic fertilizers available, it becomes desirable to know whether crop residues with high carbon-nitrogen ratios will produce organic matter when supplemented with mineral fertilizers. Again short-time experiments seem to indicate that straws and stovers supplemented with mineral fertilizers will produce large quantities of soil organic matter. Breland (1952), in a study of organic phosphorus, showed that straws and mineral fertilizers could build up the organic-matter levels in soils. Some of these data (Fig. 2) are presented in graphic form which shows the relationship between the quantities of straw and fertilizers added and the amounts of organic matter formed. Likewise, work done under greenhouse conditions seems to indicate the validity of the concept that organic matter can be formed in cultivated soils. The work of Pinck *et al.* (1948) suggests that considerable gain in both carbon and nitrogen results from additions of urea to millet residues. Table IV presents a recalculation of a portion of their data which, it should be noted, were obtained under greenhouse conditions on an Evesboro loamy sand. It will be seen that urea is quite effective in converting residues with high carbon-nitrogen ratios into soil organic matter. Some question might be raised as to whether the same results would have been secured if an inorganic nitrogen carrier had been used. It is the author's opinion that any inorganic nitrogen fertilizer would have been almost equally effective.

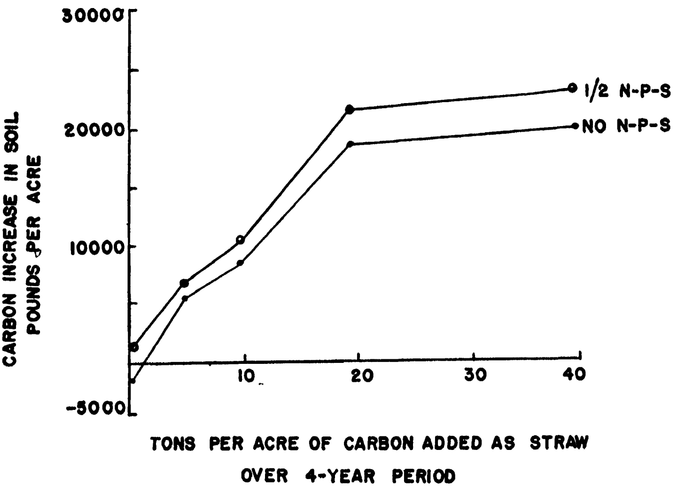

FIG. 2. Burwash plots. Soil organic matter formation with increasing carbon and fertilizer additions. (½ N-P-S means that enough nitrogen, phosphorus, and sulfur were added to convert one half of the carbon in the straw into carbon in organic matter of standard composition.)

Summarizing the place of nitrogen in the new soil cultural practices, with respect to soil organic-matter formation, the following statements by Millar and Turk (1951) cover the ground effectively. "The accumulation or organic matter in soils is primarily a nitrogen problem. Theoretically, there can be no increase in effective soil organic matter without first a proportionate increase in soil nitrogen. This implies that there is a very constant and close relationship between the nitrogen and organic matter contents in soils. This close relationship does actually exist. Since the ratio of C to N in humus is roughly 10 or 12 to 1, it must be concluded that neither carbon nor nitrogen, and hence soil organic matter, can be permanently or appreciably increased or decreased without a corresponding change in the other.

TABLE IV

Gains in Conversion of Millet to Organic Matter, under Greenhouse Conditions, with Increasing Amounts of Urea

Millet residues (mature) added, tons/acre	Nitrogen added as urea, lb./acre	Gain in carbon, tons/acre	Gain in nitrogen, lb./acre
25.0	0	2.46	329
25.0	200	2.83	406
25.0	400	3.35	447
25.0	800	3.83	532
12.5	0	1.25	171
12.5	200	1.82	276
12.5	400	2.20	330
12.5	800	2.89	402

"If the nitrogen content of plant residues is low, added nitrogen will be required to meet the demands of the soil organisms which produce the soil humus. We must, therefore, come to the conclusion that the accumulation or restoration of soil organic matter is a problem of utilizing nitrogen as a means of holding carbon and other materials that constitute humus." To this may be added the statement that organic matter is a product in the soil that should be used in crop production; therefore, it must be resynthesized as fast as it is decomposed, or faster, in order to maintain the supply and to insure that optimum soil physical conditions will prevail in the soil.

2. *Mulch Tillage Practices*

a. Living Mulches and Intercrops. Living mulches are used in row-crop production to accomplish the following objectives:

1. Increase active soil organic matter through increased residues return and adequate nitrogen use.
2. Control erosion through constant cover on the soil.
3. Control weeds through the green mulch.
4. Promote soil tilth and water conservation through the sod action of the living mulch.

The success of the living-mulch system for row-crop production depends largely upon the degree to which competition between the intercrop and the row crop can be minimized. Early experiments with living mulches and intercrops were not successful because the living mulches always reduced the yields of the row crop.

Recent studies by Kurtz *et al.* (1952a) showed that when a living mulch or an intercrop was grown between the rows of a corn crop, any competition that existed between them was largely competition for nitrogen and water. If the soil supply of nitrogen was low, then the living mulch competed heavily with the corn crop and large reductions in corn yields resulted. When adequate nitrogen and water were supplied, both crops grew well and the final corn yields were almost as good as those obtained under conventional clean cultivation. Some data from their studies are shown in Table V. The data show that under most conditions the living mulch reduced the final corn yields by about 10 per cent when adequate nitrogen and water were available. When only adequate nitrogen was supplied, the differences for intercrops varied with the season, corn grown under conventional clean cultivation yielding about 20 per cent more than under the mulch system, providing no effort was made to control the total growth of the mulch. In a dry year such as 1947 (Table V) or in areas of low rainfall, the living mulch usually competes severely with the row crop. When early-spring growth of the mulch crop was retarded by cutting or disking it before corn planting, or if the living-mulch crop was seeded after the corn crop was up, then tentative results reported by Kurtz *et al.* (1952b) indicated that there was very little reduction in the corn yields. However, these results were obtained under 36 in. of rainfall, and it is generally conceded that living-mulch systems are seldom successful in areas where the rainfall is less than 30 in.

Bray (1948) separates soil nutrients into two groups, depending on their mobility in the soil. Group one includes the immobile nutrients, such an exchangeable potassium, calcium, and magnesium, and the adsorbed and easily acid-soluble phosphorus. Available forms of these nutrients are present in the soil in quantities 5 to 20 times greater than the crop can remove in any one season. The plant roots must move toward these nutrients, because the nutrients cannot move any appreciable distance toward the roots. For nutrients of this type there is no competition, or only very little, between the living mulch and the row crop, provided the living mulch is kept out of the actual corn row or the actual root contacts are slight. Group two includes the mobile nutrients, such as nitrate nitrogen and water, which are, or can be, almost com-

TABLE V

Yields and Nitrogen Composition of Corn under Different Management Systems

	1947				1948				1949			
	Adequate nitrogen		No nitrogen		Adequate nitrogen		No nitrogen		Adequate nitrogen		No nitrogen	
Management systems	Yield, bu.	N,* %	Yield, bu.	N*, %	Yield, bu.	N*, %	Yield, bu.	N*, %	Yield, bu.	N*, %	Yield, bu.	N*, %
Continuous corn, conventional without irrigation	60	1.78	58	1.37	146	1.82	62	0.99	124	1.62	69	1.06
Continuous corn, conventional with irrigation	95	1.85	66	1.50	143	1.62	65	1.00	137	1.67	76	1.07
Continuous corn, intercrop without irrigation	34	1.88	5	1.61	106	1.65	31	0.98	104	1.62	38	1.11
Continuous corn, intercrop with irrigation	80	1.88	6	1.24	134	1.64	51	0.95	123	1.56	38	1.33

* Nitrogen expressed in per cent of dry weight of grain.

pletely removed from the soil by crops. The nitrates are free to move with, and in, the soil water, and hence one plant can almost completely denude a soil area of both nitrates and water, if both are within deficiency ranges. For these, competition exists at all times between the living mulch and the row crop. Unless the soil contains quantities of nitrogen and water sufficient for both crops, then both the row crop and the mulch will suffer.

The success of management practices and tillage systems where living mulches are used depends upon the presence of adequate nitrogen and water. This is why new tillage equipment, like the mulch planter used in living sod crops, is being advanced only as a part of an over-all management program which requires adequate fertilization practices and which is limited to areas where the rainfall is sufficient for both crops. The quantity of nitrogen needed to start such a system is usually equal to, or more than, the actual amount contained in the entire row crop. Since the mulch crop is seldom removed, the addition of nitrogen fertilizer in quantities equal to that contained in the entire row crop gives a positive balance to the soil nitrogen when crop residues are returned. As the quantity of active organic matter increases, nitrogen applications may be reduced to crop removals. This gives both nitrogen and residues for the conversion to active soil organic matter,

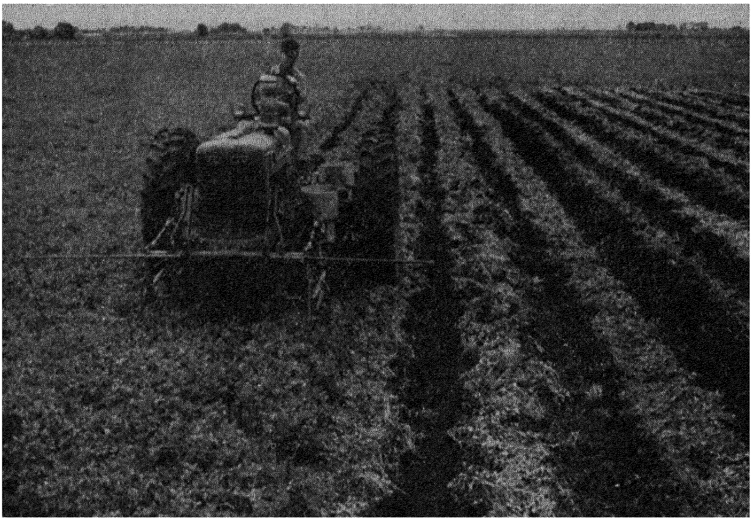

FIG. 3. Mulch planter seeding corn in established legume. Photo courtesy Paul Bateman, Agricultural Engineering Department, University of Illinois.

and the use of such a management program should lead to the maintenance of soil humus. If the mulch growth ranges from good to fair, weed control is usually adequate, and the few weeds that do grow are considered as part of the mulch system. According to Kurtz *et al.* (1952b), the mulch growth affords increased protection against erosion, maintains tilth, and increases water penetration and storage capacity of the soil.

The system of living-mulch management, using the International Harvester Company's Mulch Planter (Fig. 3) has been tried in several states. Where adequately fertilized (Fig. 4), the corn yields have usually been good. The planter destroys a narrow strip (15 to 20 in. wide) of the established sod, usually a legume, and plants the corn in this tilled strip. This keeps the intercrop out of the actual corn row and limits competition between the two crops. The undisturbed sod becomes the intercrop, or living mulch. A variation of this procedure is to seed the intercrop after the corn is up, or in the late fall. Fall-seeded mulch crops are usually rye, ryegrass, or some small grain that makes sufficient growth to afford protective cover for the soil during the winter. The following spring the winter growth is cut, disked, or

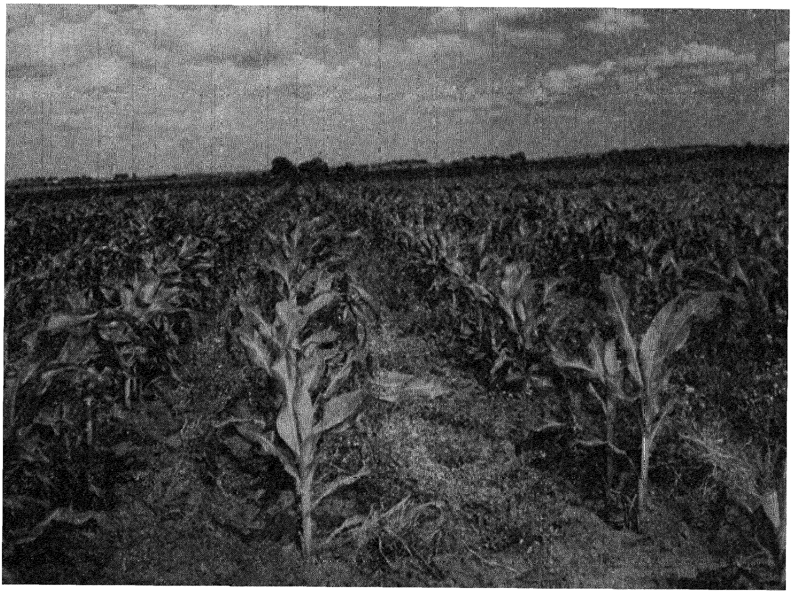

FIG. 4. Corn growing in a living mulch.

plowed, the corn mulch-planted, and the cover crop is seeded again the following fall.

Early experiments with living-mulch crops, especially legumes, indicate that planting the corn in 60-in. rows, or in 40-in. pairs 60 to 80 in. apart, is perhaps more conducive to good legume growth and high corn yields. The use of corn as a nurse crop for legumes is being studied widely and offers considerable promise for success. The livestock farmer is especially interested in a corn–legume rotation, and where it has been tried under conditions of adequate fertility, excellent corn yields and legume stands have been attained.

b. Trash Mulches and Sod Seedbeds. The trash mulches and sod seedbeds have been used to accomplish essentially the same objectives as those listed for the living mulches. They differ from the living-mulch systems because they are applicable to almost all areas, and the trash, or residue from the previous crop, is left on the surface of the soil. In some cases the practice is identical with the living-mulch system up to the time the row crop is seeded. Then the living mulch is destroyed by cultivation or chemical sprays before competition is established between the two crops. The sod-seedbed management involves chemical spraying of a previously established sod, usually a legume, and the direct seeding of either a row crop or a small grain in the undisturbed sod. In either case, the residues from the sod usually remain on the surface as protective cover. Numerous references, such as Duley and Russel (1939), Mooers *et al.* (1948), and Zingg (1950), could be cited to show the beneficial effects of trash mulches in water conservation and erosion control. The sod seedbed has the added advantage of retaining undisturbed the root systems of the sod crop. This increases materially the erosion resistance of the soil. Here, again, the management practice is associated with good fertilization programs, for when the mulch is left on the surface the previous residues do not contribute materially to the nitrogen supply needed for the cash crop. Usually, nitrogen must be added in quantities equal to the amount contained in the row crop. These trash-mulch systems should lead to greater amounts of residues being returned to the soil, to the formation of considerable active organic matter, to reduced needs for cultivation, and to increased soil conservation, as compared to the old conventional systems.

The trash-mulch systems of management are popular with those who are turning to continuous-corn or continuous-wheat rotations. For continuous corn, the cornstalks from the previous year's growth are shredded in the fall with a stalk beater, or disked to form the mulch cover. The better systems call for the fall-seeding of a cover crop, such as rye, which forms a part of the protective winter cover. This is cut, disked, or shredded the following spring; then the corn is seeded with a mulch planter. For those who do not have the mulch seeding equipment, the practice is to plow the stalks and the fall-seeded rye in the spring, and then reseed the corn with conventional equipment. This is not a true trash mulch, for the residues are plowed down in the spring. But it does permit farm operators with conventional equipment to take advantage of a fall-seeded cover crop for erosion control and to increase the quantities of residues returned to the soil. Operators who have mulch seeders usually cut or disk the fall-seeded cover crop in the spring and leave all the residues on the surface of the soil. When the trash is left on the surface some measure of weed control is achieved; however, one cultivation or chemical spraying for a good job of weed control is favored by many. Again, the system is dependent on an initial heavy fertilization program, usually 120 to 150 pounds of nitrogen to the acre, for its success as a management system. As the system becomes established, and as the active organic matter in the soil is increased, the nitrogen applications are reduced to crop removal levels. Figure 5 shows how a continuous-corn field looks just after planting with a mulch planter when no intercrop or fall seedings were used. Farmers who have tried this system are quite enthusiastic about it, and all indications point to its value for the successful control of erosion on moderate slopes.

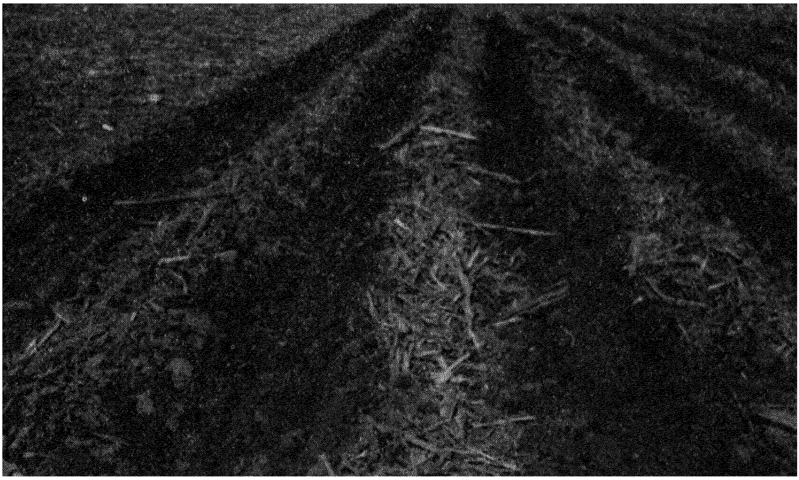

FIG. 5. Trash mulch under continuous corn without cover crop as seen at corn planting time.

The trash-mulch systems of management lend themselves very readily to row-crop production in rotations involving legumes. In the rotation system, the legume may be destroyed with chemicals, or disked, and the corn, or row crop, can be seeded directly into the sod with a mulch planter or conventional seeder. If any weeds appear, or if some of the legume survives, a single cultivation will usually afford adequate control. This gives a combination trash mulch and sod seedbed and should provide excellent erosion control, as well as maintain the favorable soil tilth established by the legume. Rotation management, as just described, should tend to conserve moisture, increase active soil organic matter, promote soil tilth, and add materially to the soil conservation characteristics of the rotation. Early reports of trials of this sort seem to indicate that yields of corn or small grains secured under trash mulches or sod seedbeds compare favorably with those secured under conventional systems of management. This type of rotation management also gives better soil protection.

3. *Soil Tilth and Erosion Control*

The literature on soil tilth studies is voluminous and may be summarized briefly by saying that soil tilth seems to be related most directly to levels of soil organic matter and to soil management practices. The work of Klingebiel and O'Neal (1952) and Van Doren and Klingebiel (1952) may be cited as among the more recent studies of this kind. In general, continuous-corn, corn-soybeans, and nonlegume rotations were shown as promoting poor soil-tilth conditions. Characteristics of the good rotations were the inclusion of a standover legume and only one corn crop in four years. Fertilizer treatments seemed to retard the rate of organic-matter depletion when the treated plots were compared with the untreated, although the organic matter may have been going down on both the treated and untreated plots, but at different rates. None of the treatments in these studies contained sufficient nitrogen to meet the needs of all of the nonlegume crops in the rotation. As a result, the most obvious differences were associated with organic matter depletion from the soil. Soils low in organic matter are usually characterized as having low permeability, being massive in structure, and being much more subject to erosion, when compared to what they were in their virgin state. This associates at least some of the loss of tilth with cultivation, and suggests that reduced tillage may be effective in the restoration of good soil tilth. The work of Klingebiel and O'Neal (1952) is of particular interest in this regard. They emphasized that the principal structural changes in soils with cropping occur in the upper 9 in., or cultivated layer, rather than at the deeper levels.

For many years it had been assumed that the very poor yields usually obtained on continuous-corn rotations were associated largely with the poor physical properties of such soils. Recent experiments, such as reported by Smith (1952), with adequate fertilizers, especially nitrogen, on infertile soils with generally poor physical characteristics show that the yields may be raised from the 40-bushel level to well over the 100-bushel level with mineral fertilization. Several such experiments have been reported in the popular press in recent years. However, no measurement of the physical changes, if any, that occurred in the surface of such soils after the addition of the fertilizer seem to have been reported. It is of interest, however, to note that the undesirable physical characteristics of these soils, if they persisted, did not appear to be reflected in yields obtained under high-fertility levels. Whether this means that the added fertilizer, which probably promoted increased microbial activity, caused an improvement in the physical conditions of the soil, or whether the physical conditions were not bad enough to be reflected in the yields, has not been definitely established. Reports of farmers' experiences seem to indicate that some improvement in physical conditions occurred after fertilization. Also, preliminary results at several erosion stations seem to indicate that with adequate fertility the amount of runoff and the erodibility of soil under continuous-corn rotations may be reduced. However, this decrease in erodibility may be due as much to increased protection afforded by the greater amounts of residues left on the soil as a result of high yields as to any improvement in physical characteristics of the soil.

Much evidence suggests that aggregate stability, and the resistance of soil aggregates to breakdown, are compatible with good tilth, or good soil physical conditions. Decomposing soil organic matter and plant residues are the source of most natural soil stabilization agents. These stabilization compounds, or cementing agents, are organic biologic residues which can be decomposed and destroyed through both tillage and microbial activity. Therefore, any good soil management program demands a large and continuous supply of actively decomposable organic matter in the soil. Since organic matter, or humus, is always undergoing decomposition, its rate of renewal should at least equal its rate of decomposition if soil tilth is to be maintained. That is why the new cultural practices stress maintenance of active organic matter and decreased tillage as essential to good soil management.

Soil erosion losses on bare corn ground, or open soybean fields, are excessive in the corn belt. The need to protect the soil against erosion, especially during the spring months, is very real. The new tillage implements and management practices that are being tested are all directed toward erosion control. That the land should be kept covered as much of the year as possible with plant growth or crop residues is a basic concept underlying the objectives of the new cultural practices. The concept is based on the assumption that effective erosion control will come through maintaining as complete protective cover on the soil as is possible at all times. This does not mean that contour farming or terracing is not essential on steep slopes. It only means that if high fertility, minimum cultivation, and protective cover are added to other well-established and reliable conservation practices, soil erosion losses may well be reduced to zero.

IV. Summary

The new tillage implements and management practices being tested in the Midwest represent a philosophy in land use, a philosophy of maximum crop production per acre of land with a minimum of soil deterioration. The philosophy is based on the concepts that high production is good for the soil, that minimum tillage promotes soil tilth and conserves soil organic matter, that high fertility promotes high yields and lessens the losses of soil humus, that large amounts of decomposable organic matter in the soil are essential to good soil tilth and good soil physical conditions, and that cover in the form of both living and trash mulches is good protection against all forms of erosion. Admittedly, the data to support these concepts, which have been discussed here, are not fully established or final, but their trends are tentatively established. The new tillage implements themselves and their use have little meaning until they are associated with soil management practices based on this philosophy of land use.

The philosophy of maximum production with minimum soil deterioration is dependent on the assumption that adequate supplies of commercial fertilizers are available for its implementation. If fertilizers are available, its implementation will raise many practical questions. For example, the value of legumes in rotations will be questioned. What is the value or benefit to be derived from certain crop sequences when the nitrogen value of the legume is removed? On any given farm, should the operator follow the same general rotation on all of the land, or should each field be considered separately and be restricted to the almost continuous growing of the crop best suited to its soil conditions? If the fields vary considerably in slope and soil characteristics, for example, the new management practices might well suggest a different crop in a continuous-cropping system for each field. Likewise, the question of the economics of buying nitrogen as compared to obtaining it by growing a legume crop will be raised. Is it justifiable to remove productive land from active production for a year in order to grow nitrogen when commercial sources are available? The answers to questions such as these will have a great influence on the popularity of these new cultural practices.

The philosophy, as represented by the new cultural practices, recognizes that the era of exploitive agriculture, on a profitable basis, is past. Since most farmers will have to buy, or grow, most of the nutrients that go into the crops they produce, maximum yields and soil conservation will become essential. The philosophy also recognizes that soil organic matter, like the other soil nutrients, is needed in crop production, and that both easily decomposable and total levels must be maintained. The land should be used fully but wisely. As yet, many of the basic concepts on which the philosophy is based are only tentative. The preliminary results, many of which are encouraging, seem to indicate that the concepts are sound and that the future will support that conclusion.

The new cultural practices being studied experimentally are attempts to apply a philosophy of maximum production with minimum soil destruction to actual farm operations. The art of making the program work has not been developed fully. It may well be that the experimental equipment now being tested will not prove satisfactory, or that the timing of some of the operations will have to be changed. But if the concepts which have been discussed continue to prove worthwhile, the art of implementing them will be developed.

V. LOOKING AHEAD

The realization that the more a soil produces the better is the care it is receiving will influence future soil management practices and tillage operations. The trend in fertilizer use will be in the direction of more and more fertility being added to soils, with special emphasis on commercial nitrogen. As the use of legumes decreases in grain systems of farming, the need for more rigid erosion control will probably stimulate the mulch type of farming. Chemical weed control will probably lessen, or even remove, the need for cultivation as a weed-control measure. The crops having the most favorable economic position in any area, for instance, cotton, corn, or wheat, will tend to become continuous crops on the least erosive lands. Similarly, if the farmers' economic position continues to drop, or if farm labor continues to be in short supply, the demand for once-over tillage equipment will increase. This does not mean that the plow or disk will disappear from the farm. The need to turn under crop residues, or incorporate them into the soil, will still exist. The frequency of plowing will be reduced, but the need for a tool that will do just what the plow now does so well will still exist.

The future holds the answer to many questions relative to these new cultural practices. One such question is whether there is any good reason why efforts should be made to increase or maintain the organic matter in the soil. Others are: what is the cost of producing a ton of soil organic matter? can soil conditioners be substituted more economically? what are the minimum quantities of active soil organic matter consistent with good tilth? what is the value of restoring good tilth to a potentially high-producing soil when its high fertility has been restored? and what will be the insect and disease problems with intensive growing of one crop? For the moment it must be assumed, for lack of definite data to the contrary, that maintaining soil organic matter and supplying residues for active decomposition are desirable and economical practices and that the restoration and maintenance of soil tilth are necessary for good soil management.

REFERENCES

Bray, R. H. 1948. "Diagnostic Technique for Soils and Crops," pp. 53–86. American Potash Institute, Washington, D. C.

Breland, H. L. 1952. Ph.D. Thesis, Department of Agronomy, University of Illinois, Urbana, Illinois.

Duley, F. L., and Russel, J. C. 1939. *J. Am. Soc. Agron.* **31**, 703–715.

Klingebiel, A. A., and O'Neal, A. M. 1952. *Soil Sci. Soc. Amer., Proc.* **16**, 77–80.

Kurtz, T., Melsted, S. W., and Bray, R. H. 1952a. *Agron. J.* **44**, 13–17.

Kurtz, T., Melsted, S. W., Bray, R. H., and Breland, H. L. 1952b. *Soil Sci. Soc. Amer., Proc.* **16**, 282–285.

Lee, C. K., and Bray, R. H. 1949. *Soil Sci.* **68**, 203–212.

Millar, C. E., and Turk, L. M. 1951. "Fundamentals of Soil Science," p. 257. John Wiley & Sons, New York.

Miller, L. B. 1951. Illinois Agr. Expt. Sta. Mimeo., AG1481.

Mooers, C. A., Washko, J. B., and Young, J. B. 1948. *Soil Sci.* **66**, 307–315.

Pinck, L. A., Allison, F. E., and Gaddy, U. L. 1948. *J. Am. Soc. Agron.* **40**, 237–248.

Smith, G. E. 1952. *Missouri Expt. Sta. Bull.* **583**.

Van Doren, C. A., and Klingebiel, A. A. 1952. *Soil Sci. Soc. Amer., Proc.* **16**, 66–69.

Zingg, A. W. 1950. *Soil Sci. Soc. Amer., Proc.* **15**, 11–17.

Seed-Flax Improvement

Co-ordinated by J. O. CULBERTSON

United States Department of Agriculture, St. Paul, Minnesota

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I. INTRODUCTION

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The flax plant (*Linum usitatissimum* L.) produces two valuable products, flaxseed and fiber. Seed-flax or linseed types are grown principally for their seed, although some use is made of the fiber in producing high-quality specialty papers. Fiber-flax types, on the other hand, are grown for the high-quality fibers from which linen yarn is spun. Seed produced on fiber varieties and not required for sowing is crushed for its oil. Flax production in the United States is limited almost entirely to the seed-flax types. The seed is crushed and a high-quality drying oil is obtained which is used in making paint, varnish, linoleum, oilcloth, printer's ink, and a number of minor products. Of the total linseed oil used by industry, about 75 per cent is consumed in the manufacture of paint and varnish and about 12 per cent in linoleum and oilcloth.

It formerly was necessary for the United States to import an appreciable amount of the linseed needed for industry either as seed or oil. During the past ten years, however, domestic production has exceeded consumption and some flaxseed or linseed oil has been exported. In the ten-year period 1944–1953, annual production averaged 36,371,000 bushels from 3,834,000 harvested acres, with an average yield of 9.4 bushels per acre.

The total consumption of fats and oils by the drying-oil industries has varied considerably from year to year, ranging from a low of about 700,000,000 pounds in 1938 to over 1,000,000,000 pounds. Linseed oil has made up from 48 to 85 per cent of the total amount of drying oils used by industry. Since 1946 there has been a significant increase in the use of soybean, tung, and tall oils by the drying-oil industry.

Although seed-flax may be grown in many states, over 95 per cent of the crop has been grown in the six states of North Dakota, Minnesota, South Dakota, Iowa, Montana, and Wisconsin. The concentration of acreage in these states has been due largely to conditions favorable to flax growing, such as moderate summer temperatures and sufficient but not excessive moisture to assure a good yield. A considerable acreage is grown in Texas as a fall-sown crop that matures before summer temperatures become excessive. Flax also is grown in California and Arizona as a fall-sown crop under irrigation, where average yields of 35 bushels per acre have been attained and individual yields of over 70 bushels have been recorded.

Advances in flax production have been attained through a combination of better cultural methods, especially weed control, control of destructive diseases, and the development of superior varieties.

Dillman (1936) in the U. S. Dept. Agr. Yearbook discussed the history of flax-growing in the United States rather fully and showed the progress made in breeding superior varieties up to that time. This paper will deal with advances made in flax production since 1936.

II. Storage Properties of Flaxseed

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1. Introduction

Flaxseed, in common with other grains, has excellent keeping qualities when stored in a relatively dry state but, after unfavorable harvesting conditions, the moisture content may be sufficiently high to permit deterioration. The problem of storing grains without serious loss in quality is not new, but its importance has been greatly increased in recent years by the development of more economical methods of harvesting and transportation. Before the days of the combine harvester, grain was allowed to dry in field shocks before threshing and presented little difficulty in storage. With the combine, particularly during wet seasons, grain which contains excessive moisture for safe storage may be harvested. The transportation and storage of larger and larger masses of grain have augmented the storage hazards, and increased attention is now being given to studies on the underlying factors involved in the deterioration of grain in storage. In comparison with other grains, few researches have been carried out with flaxseed; this is perhaps a reflection of the fact that for many years the United States demand greatly exceeded domestic production and stocks were not carried in storage over long periods. However, the factors involved in the deterioration of all grains are similar, and research findings with various seeds may be employed to advantage in any discussion of grain storage.

Numerous investigations have shown that moisture content is the predominant factor in determining the keeping quality of grain, but other factors, such as temperature, oxygen supply, inherent characteristics and soundness of the grain, length of storage, presence of molds and insects, influence the extent of the biochemical changes which take place. Observations during the commercial handling and storage of grain are of limited value in determining the relative significance of these various factors. Since grain, although it is stored in the dormant state, contains living protoplasm and is almost invariably contaminated with various species of molds and sometimes insects as well, a study of the rate of respiration provides a convenient laboratory method for investigating the factors involved in the deterioration of stored grain. In laboratory experiments, the quantity of heat produced is very small and is so difficult to measure that the production of carbon dioxide has been the most commonly used criterion of potential keeping quality under various experimental conditions.

2. *Grain Respiration and Its Measurement*

In the presence of oxygen, that is, under aerobic conditions, respiration involves the oxidation of organic constituents of the seed, particularly carbohydrates and fats, with the formation of carbon dioxide and water as the ultimate end products. The complete oxidation of a typical carbohydrate and fat is represented by the following equations:

Glucose

$$\begin{array}{ccccccccc} C_6H_{12}O_6 & + & 6O_2 & = & 6CO_2 & + & 6H_2O & + & 677.2\ \text{Cal.} \\ 180\ \text{g.} & & 134.4\ \text{l.} & & 134.4\ \text{l.} & & 108\ \text{g.} & & \end{array}$$

Tripalmitin

$$\begin{array}{ccccccccc} (C_{15}H_{31}COO)_3C_3H_5 & + & 72.5O_2 & = & 51CO_2 & + & 49H_2O & + & 7616.7\ \text{Cal.} \\ 806.8\ \text{g.} & & 1624\ \text{l.} & & 1142.4\ \text{l.} & & 883\ \text{g.} & & \end{array}$$

In the complete oxidation of glucose the consumption of 1 l. of oxygen and the production of 1 l. of carbon dioxide under standard conditions (0° C. and 760 mm. pressure) corresponds to the liberation of 5.04 Cal.; in the complete oxidation of tripalmitin 1 l. of oxygen is equivalent to 4.69 Cal. and 1 l. of carbon dioxide to 6.67 Cal. In the oxidation of glucose, the respiratory quotient, or R.Q. (the ratio of the moles or volumes of carbon dioxide produced to the moles or volumes of oxygen consumed), is unity, whereas that for the oxidation of tripalmitin is 0.70. The respiratory quotient alone, however, cannot be relied upon to furnish precise information concerning the nature of the materials being respired by seeds, since it is influenced by a number of factors such as the transformation of carbohydrates to fats and of fats to carbohydrates and the formation of organic acids. Oxidation of plant materials may take place without the use of molecular oxygen—a phenomenon which occurs under anaerobic conditions. This is the type of respiration which occurs in the process of fermentation carried out by many microorganisms to produce such end products as carbon dioxide, ethyl alcohol, and various organic acids.

Two general methods have been used in measuring the respiration of dormant seeds. In one the seeds are maintained in a closed container for a suitable interval of time after which the carbon dioxide, and sometimes the oxygen content also, is determined. An effort is usually made to avoid inhibitory concentrations of carbon dioxide by varying the sample weights or storage periods in accordance with the respiratory activity. This procedure has been used by Bailey (1940) in comparing the respiration of cereal grains and flaxseed. In the other general type of procedure, the seeds are aerated with carbon dioxide-free air of a relative humidity which will maintain the moisture content of the seeds at the desired level. The air which is withdrawn from the respiration chambers is measured and analyzed for its oxygen and carbon dioxide content. By employing sufficient aeration, trials may be conducted over extended periods without danger of partial inhibition of respiration. Milner and Geddes (1945) and Schricker (1948), among others, have described apparatus for carrying out respiration trials in this manner.

3. *General Features of Grain Respiration*

In dry grain devoid of insects the rate of respiration per unit weight of dry matter is low and increases very slightly as the moisture content is gradually raised until a certain critical moisture range is reached; with further increases in moisture, the respiration is markedly accelerated and heating tendencies appear. This characteristic feature of grain respiration is well illustrated in Fig. 1, taken from studies reported by Bailey (1940) in which the respiration trials were conducted in a closed system for a fixed time interval. Although all grains gave curves of the same general shape, the different species exhibited somewhat different critical moisture values. Marked acceleration in the respiration of the various cereals occurred at moisture contents of 14 to 15 per cent; flaxseed was conspicuous by exhibiting a much higher respiratory rate than the cereal grains with a critical moisture value somewhat below 11.0 per cent. The moisture levels at which increases in respiratory rate occurred approximate those above which heating and spoilage of these grains are frequently encountered in commercial storage.

In respiration trials in which grains have been aerated, low and virtually constant respiratory rates have been obtained over several days when the moisture contents were below or only slightly above the critical levels. Increases in moisture content above these values are accompanied by accelerations in the rate of respiration, after which equilibrium conditions are again approached. This has been shown by

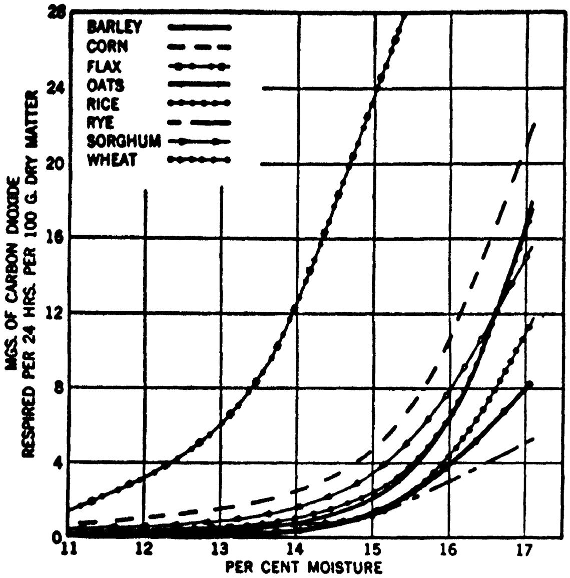

Fig. 1. Comparative respiration of various cereal grains and flaxseed at 37.8° C. (100° F). Data of Bailey (1940).

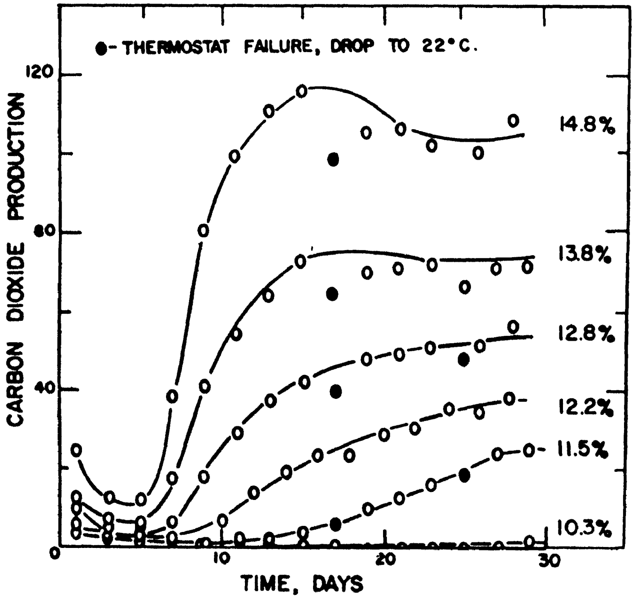

Fig. 2. Effect of moisture content and time on the respiration of flaxseed at 25° C. The respiratory rate is expressed as mg. CO_2 per 100 g. flaxseed (dry matter) per 24 hours.

Milner and Geddes (1946) for soybeans, by Milner *et al.* (1947a) for wheat, and by Larmour *et al.* (1944) and Schricker (1948) for flaxseed. Typical data obtained by Schricker are shown in Fig. 2.

4. *Role of Microorganisms*

The total respiration of a particular lot of grain free from insects may arise from the biological processes of the seeds themselves and of the microorganisms which are invariably present on the surface of grain and under the seed coat. Several early investigators noted the presence of fungi in spoiled or heating grain and in recent years evidence has been accumulating that the sharp increases in dormant seed respiration which occur above certain moisture contents are due to the growth of saprophytic molds on and within the grain. (Gilman and Barron, 1930; Larmour *et al.*, 1935; Leach, 1944; Milner and Geddes, 1945, 1946; Nagel and Semeniuk, 1947; Semenuik *et al.*, 1947; Gilman and Semenuik, 1948; Schricker, 1948; Bottomley *et al.*, 1950.) The moisture content of grain undergoing bulk storage is seldom high enough to support bacterial growth, since it must approach equilibrium with an atmosphere of about 95 per cent relative humidity. Although various grains have different critical moisture levels, it is significant that they all correspond rather closely with the moisture content which these grains would attain when exposed to a relative humidity of about 75 per cent. Thus the equilibrium moisture at this humidity at 25° C. is about 14.5 per cent for wheat (Coleman and Fellows, 1925); 10.5 per cent for flaxseed (Coleman and Fellows, 1925; Schricker, 1948; Larmour *et al.*, 1944); 14 per cent for soybeans (Ramstad and Geddes, 1942); 13 per cent for rough rice (Karon and Adams, 1949); and 14 per cent for shelled corn (Koehler, 1938). Several investigators, including Lea (1933), Galloway (1935), Haines (1937), Smith (1938), Barton-Wright and Tomkins (1940), and Macara (1943), have shown that over relatively short time intervals a relative humidity of 75 per cent is about the minimum for the germination of mold spores at ordinary temperatures in the presence of nutrients. However, Snow *et al.* (1944) have found that after a very prolonged latent period molds grow at relative humidities as low as 65 per cent. The respiration-time curves for high-moisture grain are similar in form to a microbiological population growth curve. At moisture contents below those at which molds will germinate, the respiration is due to the biological processes of the grain itself and remains relatively constant from day to day. A similar constancy in respiration rate is obtained when grain of high moisture content respires under nitrogen or in the presence of fungistatic agents which have little or no effect on germination (Milner, 1946; Milner *et al.*, 1947b; Matz and Milner, 1951).

Various species of molds differ appreciably in their minimum moisture requirements; for instance, Semeniuk, Nagel, and Gilman (1947) have reported *Aspergillus candidus* to germinate at 72.5 per cent relative humidity, *A. niger* at 80.0 per cent, *A. flavus* at 82.5 per cent, *Penicillium chrysogenum* at 85.0 per cent, and others at 87.5 per cent. It is not surprising, therefore, that the preponderance of different species varies with the moisture content at which the grain is held. Milner *et al.* (1947a) observed that the extremely xerophytic mold, *A. glaucus*, predominated on wheat samples up to 16.8 per cent moisture (83 per cent relative humidity), whereas at higher moisture levels *A. candidus*, along with some Penicillia, became prominent. *A. flavus* became the major organism at moisture values in excess of 25 per cent. No detailed studies of the numbers and kinds of molds involved in the respiration of flaxseed have been reported.

5. *Biochemical Changes Associated with Respiration*

The rates at which chemical changes occur in stored grain are determined by the moisture content, the storage temperature, the oxygen supply, and the degree of soundness of the grain. Most of the changes are enzymic in nature and result from the action of the enzymes of the grain and of the fungi associated with it. Grain which is stored at moisture levels and temperatures below which microorganisms grow undergoes chemical changes very slowly, but when conditions are favorable for their development, extensive deterioration may occur, as evidenced by marked losses in viability, increases in fat acidity, decreases in nonreducing and total sugars, lowered processing value, and heat damage in the more advanced stages. The various chemical and nutritive changes which occur have been reviewed by Zeleny (1948).

Carbohydrates appear to be the first seed constituents which are utilized in the respiratory processes, and this results in an apparent increase in other constituents such as fat and protein. Studies with various grains have shown that increases in fat acidity invariably occur upon storage, and Zeleny (1940, 1948) regards the determination of fat acidity as the best index of the soundness or condition of grain, since it serves as a measure of the deterioration that has already occurred. Discrepancies in the use of fat acidity as an index of storage deterioration may be due to differences in the conditions required for maximum activity of the lipases of the grain and of the molds and to the number and types of molds which are present. It has been shown too that actively growing molds can metabolize the fatty acids to produce acetone and carbon dioxide (Mukherjee, 1952), and hence deterioration induced by molds may progress without an appreciable increase in fat acidity. Among the changes which occur in oil seeds is a decrease in the iodine number of the oil. This is illustrated in Table I, which shows

TABLE I

Biochemical Changes in Flaxseed Due to Respiration at Various Moisture Levels for 29 Days at 25° C.

Moisture content		Total CO_2 production*	Respiratory quotient average	Non-reducing sugars, %	Oil iodine value (Wijs)	Fat acidity†
Initial, %	Final, %					
Original	Sample	—	- -	1.2	185	2.3
10.3	11.3	0.06	- -	1.2	185	2.3
11.5	11.7	0.25	0.60	1.2	180	6.0
12.2	12.3	0.60	0.50	1.3	178	6.0
12.8	13.4	0.90	0.75	1.1	173	7.9
13.4	15.4	1.58	0.75	1.0	163	11.2
14.8	16.4	2.56	0.75	1.0	160	12.5

* Expressed as g. CO_2 per 100 g. flaxseed (dry matter basis).

† Expressed as mg. KOH required to neutralize the free fatty acids in 1 g. oil.

certain of the data obtained by Schricker (1948) on flaxseed after the respiration trials illustrated in Fig. 2.

6. Prevention of Deterioration

The limited respiration trials which have been conducted on flaxseed indicate that it is a more hazardous crop to store than the cereal grains, and deterioration may occur if the moisture content exceeds about 10.5 per cent. Although moisture content is the major factor in determining the storage behavior of grain, it is also influenced by the temperature, the oxygen supply, the nature of the fungi present, and the previous treatment and condition of the grain both of which may affect the availability of nutrients, the mass of grain, and the length of storage. Grain has a low specific heat and if heat is produced more rapidly than it is dispersed by the low rate of thermal conduction through the grain, by radiation, by conduction and convection in the interseed air, and by evaporation of moisture, the temperature of the grain will rise (Oxley, 1948). This results in an increase in the rate of respiration so that a continuously accelerating process takes place and "spontaneous heating" occurs. When the temperature rises sufficiently high to inactivate the enzymes and put an end to the biological phase of heating through the cessation of respiration, a secondary spontaneous heating occurs owing to nonbiological oxidation. This has been demonstrated under conditions of adequate aeration in the laboratory with soybeans (Ramstad and Geddes, 1942; Milner and Geddes, 1946); wheat (Milner *et al.*, 1947a), and flaxseed (Schricker, 1948), employing calorimeters which are so constructed that as the grain heats, the temperature of the atmosphere outside the container is automatically raised to keep in step with that of the grain.

Researches with various grains reveal that the respiration of the dormant seeds is low, and most workers hold the view that the initiation of heating in stored grain is due primarily to the much greater respiration of actively growing molds. This has stimulated studies with various mold inhibitors (Milner, 1946; Altschul *et al.*, 1946; Milner *et al.*, 1947b; Matz and Milner, 1951) and with storage under an inert atmosphere. These procedures are not commercially feasible for the prolonged storage of high-moisture grain. Dusting grain with solid fungicidal or fungistatic agents does not prevent the activity of the subepidermal microflora or of the seed enzymes and unless the chemicals could be removed, the grain would be unsuitable for many biological purposes. Storage of comparatively dry grains in an inert atmosphere or one deprived of oxygen has been effective in preventing losses in viability and inhibiting undesirable chemical changes in seed (Vayssière, 1948; Schricker, 1948), but this type of storage cannot be recommended for high-moisture grain because of the danger of deterioration due to anaerobic respiration. In the light of present knowledge, drying grain to a moisture content that is in equilibrium with an atmosphere of less than 75 per cent relative humidity is the only safe way to store grain.

III. FLAX RUST

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1. *General*

Rust, *Melampsora lini* (Pers.) Lév., the most destructive disease of flax, occurs throughout the important flax-growing regions of the world. It occurs as intermittent epiphytotics in most areas. In the United States flax was heavily damaged in 1928, 1941, 1942, 1943, 1950, and 1951. The loss in 1951 exceeded $10.000.000. Prasada (1948) reported rust a limiting factor in flax production in India, where it causes enormous losses annually.

The succumbing of "rust-resistant" varieties to rust in the North

Central States emphasizes the need for basic studies on physiologic specialization. BISON, released in 1927 as a rust-resistant variety, was grown almost to the exclusion of other varieties in the late 1930's. However, in the early 1940's it was so heavily damaged by rust that by 1944 it had passed out of the picture as an important variety. KOTO, developed as a rust-resistant replacement for BISON, was immune from rust during several years of nursery tests throughout the North Central States, but rusted severely while being increased for distribution in 1943. DAKOTA, released in 1946, carried the Newland gene for rust reaction. For more than 30 years this gene had conditioned immunity from North American rust races, but in 1948 rust was found on DAKOTA in Minnesota and North Dakota. The new races spread rapidly and were so destructive that by 1952 the rust-resistant varieties B5182, MARINE, REDWOOD, ROCKET, and SHEYENNE had replaced most of the DAKOTA.

Flax rust attacks only flax. It is eu-autoecious, that is, all stages of its life history are found only on the flax plant. In a mild climate it may live from one crop year to the next in the uredial or repeating stage on volunteer (Vallega, 1938) or wild flax (Waterhouse and Watson, 1944). In a more rigorous climate, such as that of the North Central States, it overwinters as telia on stubble or straw left in the field or on bits of straw in uncleaned seed. The teliospore germinates by producing a promycelium which usually bears four haploid sporidia. The pycnium develops from a sporidial infection. Pycnia are of two types or sexes. No further development occurs unless pycniospores from a pycnium of one sex are transferred to a pycnium of the other sex. Then an aecium bearing aeciospores develops at the pycnium. Aeciospore infection gives rise to a uredium. A uredial generation may be repeated about every 10 days. Telia are formed in the older uredia. Consequently, there is no alternate host "weak link" in the life cycle of flax rust. In the rusts of cereals, the destruction of an alternate host eliminates sexual reproduction with its potentialities of hybridization and mutation. In the case of the eu-autoecious flax rust, however, in the North Central States, hybridization probably is concomitant with each year's initial infection.

2. *Physiologic Races*

Physiologic specialization in flax rust was first demonstrated by Flor (1935), who differentiated 14 races by the reaction of 9 flax varieties. Using additional differential varieties, Flor (1940) identified 10 additional races.

Wherever studied, flax rust has been found to be highly specialized. Physiologic specialization has been demonstrated in Europe by Straib

(1939a, b), in Australia by Waterhouse and Watson (1944), in Argentina by Vallega (1938, 1944), and in New Zealand by Cruickshank (1952).

Flax varieties resistant in one region may be susceptible in another. BISON has been susceptible to all rust collections in Europe, North America, and South America, but Waterhouse and Watson (1941) found it immune from Australian collections of rust. They increased their rust cultures on BOMBAY, the variety found by Vallega (1944) to possess the only gene conditioning immunity in South America. All flax varieties now grown in the North Central States are highly susceptible to races occurring in South America.

3. *Sources of Resistance to Rust*

The flax rust differentials, in common with the varieties serving to identify physiologic races of other pathogens, were selected by empirical trials. The reaction of approximately 200 varieties grown in the Flax Classification Nursery to various rust collections was determined. These varieties had been chosen for diverse type and origin and avoidance of duplicates from more than 1300 accessions secured from the major flax-producing regions of all the continents. Flor (1940) found most of the varieties mixed for rust reaction as did Dillman (1953) for type. However, in most cases the reaction of the individual plant was pure. This would be expected with a closely self-pollinated crop. Varieties showing differentiating potentialities were purified by line selection and used as differentials, if warranted by further testing.

The reactions of numerous commercial and experimental varieties to native races of rust have been listed by Vallega (1938, 1944) in Argentina, by Straib (1939b) in Europe, by Waterhouse and Watson (1944) in Australia, and by Prasada (1948) in India. Flor (1940) classified 201 flax varieties, including those grown by Dillman (1953) in the Flax Classification Nursery of the United States Department of Agriculture, according to their reaction to 13 North American and 3 South American races. No variety was resistant to all races, but no race was capable of attacking all varieties.

4. *Inheritance of Pathogenicity*

By inbreeding races of flax rust Flor (1942) showed that heterozygosity in both North American and South American races was common. This was to be expected, because an open fertilizing procedure, the transfer of pycniospores from one haploid pycnium to another, precedes the initiation of each culture.

Urediospores have the same pathogenicity as the aeciospores from which they are derived (Flor, 1941). However, aeciospores may not be able to reinfect the variety on which they develop. The F_1 generation aeciospores of the cross of race 22 with race 6, although produced on Ottawa 770B, were incapable of reinfecting Ottawa 770B. Apparently the dicaryotic aecium continues to be nourished by the haploid mycelium of the maternal pycnium.

In crosses between North American races and between North American and South American races Flor (1942) found virulence to be recessive, except for the gene found in WILLISTON BROWN. Thus, the F_1 culture of the cross of race 22 with race 24, which between them attacked 15 of 16 differentials, attacked only the 3 that were susceptible to both parent races. Consequently, a pathogenicity test of a uredial culture may be no indication of the virulence of its progeny.

In a study of the cross of race 6 with race 24 Flor (1942) found that the F_2 cultures segregated for pathogenicity on AKMOLINSK, BOMBAY, and BUDA. The segregation ratio was explained by assuming that two pairs of quantitative genes conditioned infection type on BUDA, that single independent pairs of genes, with avirulence dominant, conditioned infection types on AKMOLINSK and BOMBAY, and that the pair of genes conditioning infection type on AKMOLINSK was linked with one of the pairs of genes for pathogenicity on BUDA.

Flor (1946) reported on the genetics of pathogenicity in crosses between race 22 and races 6 and 24. Race 22, of South American origin, attacked 14 of the 16 rust differential varieties then in use. BOMBAY and J.W.S. were resistant to it. Race 6 attacked only WILLISTON GOLDEN and WILLISTON BROWN. Selfing studies had shown race 6 to be heterozygous for virulence on AKMOLINSK, and one of the three F_1 cultures of the cross of race 22 × race 6 attacked AKMOLINSK in addition to WILLISTON GOLDEN and WILLISTON BROWN, the differentials susceptible to both parent races.

The F_2 cultures of race 22 × race 24 segregated for pathogenicity into ratios indicative of the number of genes possessed by each differential which were effective in conditioning resistance to the avirulent parental race. The ratios approximated 3 avirulent to 1 virulent on Ottawa 770B, NEWLAND, BOMBAY, PALE BLUE CRIMPED, KENYA, AKMOLINSK, ABYSSINIAN, LEONA, and TAMMES PALE BLUE, 15 avirulent to 1 virulent on BOLLEY GOLDEN and ITALIA ROMA, and 63 avirulent to 1 virulent on MORYE. Pathogenicity on Ottawa 770B, NEWLAND, and BOMBAY was independently inherited. Pathogenicity on PALE BLUE CRIMPED and KENYA, on AKMOLINSK, ABYSSINIAN, and LEONA, and on WILLISTON GOLDEN and WILLISTON BROWN was inherited on a unit basis. WILLISTON GOLDEN and WILLISTON BROWN have a common gene for resistance to some F_2 cultures of this cross. One of the pairs of genes for virulence on BOLLEY GOLDEN was the same as one of the pairs of genes for virulence on ITALIA ROMA or was closely linked with it. The pair of genes conditioning virulence on TAMMES PALE BLUE was either the same as one of the three pairs of genes for virulence on MORYE or was closely linked with it.

Analysis for independent assortment of pathogenic characters showed that 768 races were theoretically obtainable from the cross of race 22 with race 24. From the 133 F_2 cultures studied, 64 races were identified, of which 62 were new. None of the progeny approached race 22 in width of virulence. At the same time, there was no indication of allelic or linkage relations between the genes for virulence on BOMBAY, attacked by race 24, and any of the genes for virulence on the 14 differentials susceptible to race 22. Therefore, a race attacking all the differentials except J.W.S. should be obtainable from this cross.

Except for two deviations, both readily explainable, the pathogenicity of the race 6 × race 22 hybrids was the same as that of the race 22 × race 24 hybrids. Three F_2 progenies of race 6 × race 22 were studied. The F_1 and the 74 F_2 cultures of Hybrid A attacked AKMOLINSK. Therefore, in Hybrid A virulence on ABYSSINIAN and LEONA was inherited as a unit. AKMOLINSK was resistant to the F_1 of Hybirds B and C, and in these hybrids virulence on AKMOLINSK, ABYSSINIAN, and LEONA was inherited as a unit as in the cross of race 22 × race 24. F_2 cultures of the three progenies of race 6 × race 22 segregated for virulence on TAMMES PALE BLUE in a bifactorial ratio, and no culture attacked MORYE. In subsequent investigations, it has been found that both TAMMES PALE BLUE and MORYE possess the KOTO gene. KOTO is susceptible to races 22 and 24 but is resistant to race 6. Consequently the KOTO gene was not effective in the race 22 × race 24 hybrids but was effective in the race 6 × race 22 hybrids. Against race 6 TAMMES PALE BLUE had two effective genes and MORYE had four.

The 98 F_2 cultures of hybrids of race 6 with race 22 yielded 39 different races of which 36 were new.

5. *Inheritance of Resistance*

Henry (1930) found that immunity from a North American rust collection was dominant and conditioned by single genes in Ottawa 770B and BOMBAY and by two genes in an Argentine selection. Myers (1937) in crosses involving 17 flax varieties explained his results by assuming that the genes for reaction to North American races of rust lay in two allelic series, *L* and *M*. Immunity was dominant and less resistant types were hypostatic to more resistant ones. Flor (1947) studied the interaction of genes conditioning rust reaction in 20 flax varieties, including the 16 varieties then used as rust differentials. Greater resistance was dominant to lesser resistance. By the use of selected races of rust, 19 different genes were found to condition reaction to rust in the 16 differential varieties. Of these 19 genes, 7 were in the *L* series of alleles, 4 were in the *M* series of alleles, 5 were in the chromosome carrying the BOMBAY *N* gene, and 3 were not definitely located. As crossing over occurred between some of the genes in the *N* series, future studies may necessitate revision of the symbols for these genes. Kerr (1952) used several Australian races in genetic studies of rust resistance in flax. Results with Australian race K closely paralleled those of Flor (1947) in the United States. The resistance of BISON to Australian race A was due to a single dominant gene in the *L* series. Ottawa 770B and NEWLAND each carry a gene for resistance to race A apparently in the *N* series, additional to those determined in the United States. The additional Ottawa 770B gene also was effective against Australian race E.

6. *New Differentials Carrying Single Rust-Conditioning Genes*

There appears to be a gene for gene relationship between resistance in the host and virulence in the pathogen. Races of wide host range are homozygous for a large number of recessive genes for virulence. A variety is attacked only by races possessing the specific gene or genes for virulence on it. A differential with two resistant genes cannot differentiate races attacking either or neither of its resistant genes. Consequently, a series of differentials each possessing one unique rust-conditioning gene would facilitate race identification and the detection of new genes for virulence.

A variety with a single rust-conditioning gene that is either highly resistant or highly susceptible to all races makes an ideal differential. A series of such differentials possessing all the important rust-differentiating genes would make an ideal set of differentials. However, it will probably remain a theoretical concept. Resistant genes are identifiable only by races unable to attack them. Exhaustive tests give no assurance that a variety may not possess a gene ineffective against all races with which it has been tested but effective against those occurring in some other region. The resistance of BISON and the existence of two pairs of genes in Ottawa 770B and NEWLAND for resistance to Australian race A as reported by Kerr (1952) illustrate this point.

A series of host testers each possessing a unique rust-conditioning gene should facilitate the development of rust-resistant varieties. They also may be essential to the solution of such fundamental problems as the role of adaptation, hybridization, and mutation in the origin of new races and the discovery of the nature of physiological resistance. Consequently Flor (unpublished) revised the flax rust differential varieties.

The 18 varieties of flax now serving to differentiate races of flax rust are listed as "New" in Table II, together with 14 supplemental

TABLE II

Origin and Probable Genotype of Flax Rust Differential Varieties

Differential varieties	C. I. No.	Parent differential variety	C. I. No.	Probable genotype
New:				
OTTAWA 770B	355	OTTAWA 770B	355	$LL\ mm\ nn$
DAKOTA	1071	NEWLAND	188	$ll\ MM\ nn$
BOMBAY	42	BOMBAY	42	$ll\ mm\ NN$
STEWART	1072	J.W.S.	708-1	$L^2L^2\ mm\ nn$
CASS	1182	BOLLEY GOLDEN	644	$ll\ M^3M^3\ nn$
KOTO	842	MORYE	112	$ll\ mm\ N^6N^6$
CLAY	1188	MORYE	112	*
POLK	1191	VICTORY	1045	$ll\ mm\ N^5N^5$
BIRIO	1085	RIO	280	$L^6L^6\ mm\ nn$
KENYA	709-1	KENYA	709-1	$L^4L^4\ mm\ nn$
AKMOLINSK	515-1	AKMOLINSK	515-1	$ll\ mm\ N^1N^1$
ABYSSINIAN	701	ABYSSINIAN	701	$ll\ mm\ N^2N^2$
LEONA	836	LEONA	836	$ll\ mm\ N^3N^3$
WILDEN	1193	WILLISTON GOLDEN	25-1	$L^5L^5\ mm\ nn$
WILLISTON BROWN	803-1	WILLISTON BROWN	803-1	$ll\ M^1M^1\ mm$
VICTORY A	1170	VICTORY	1045	$ll\ M^4M^4\ nn$
BOWMAN	1184	BOLLEY GOLDEN	644	*
BISON	389	BISON	389	$L^9L^9\ mm\ nn$
Supplemental:				
BURKE	1180	BUDA	270-1	$L^1L^1\ mm\ nn$
WARD	1181	BUDA	270-1	$ll\ M^2M^2\ nn$
PALE BLUE CRIMPED	647	PALE BLUE CRIMPED	647	$L^3L^3\ mm\ nn$
NORMAN	1186	ITALIA ROMA	1005-2	$ll\ mm\ N^7N^7$
BOLLEY GOLDEN SELECTION	1183	BOLLEY GOLDEN	644	†
GRANT	1194	TAMMES PALE BLUE	333-1	†
MARSHALL	1335	TAMMES PALE BLUE	333-1	$ll\ mm\ N^4N^4$
ARGENTINE SELECTION	705	ARGENTINE SELECTION	705	†
LINO M. A. 6899	868	LINO M. A. 6899	868	†
CORTLAND	1512	PALE BLUE VERBENA	416-3	$ll\ M^5M^5\ nn$
MINNESOTA SELECTION	438	MINNESOTA SELECTION	438	L^7L^7 — —
BARNES	1190	MINNESOTA SELECTION	438	†
MINERVA	1081	MINERVA	1081	†
TOWNER	1561	BISBEE	1336	$L^8L^8\ mm\ nn$

* Either outside the L, M, or N chromosomes or in the N chromosome with a high percentage of crossing over.

† Not known.

differentials, the parent variety from which the new line was derived, and the probable rust genotype where known. Most of the new lines were secured by utilizing the selectivity of F_2 cultures of race 22 × race 24 and of race 6 × race 22 in isolating lines with single rust-conditioning genes from the progeny of crosses of the original differentials with BISON. Seven of the new differential lines have been resistant to all North American races, 3 possess genes for resistance to some North American races that are found in varieties now grown commercially, and 8 have been most useful in differentiating races of rust throughout the world.

Varieties listed as supplemental differentials are considered to be less satisfactory and include some varieties used by other investigators to differentiate their local races.

Ottawa 770B, CASS, POLK, BIRIO, KENYA, LEONA, BOWMAN, PALE BLUE CRIMPED, BOLLEY GOLDEN SELECTION, MARSHALL, CORTLAND, and TOWNER have been highly resistant to rust in the field in the North Central States. Consequently, there appears to be an ample reserve of resistant germ plasm. However, all of these varieties are susceptible to races of flax rust known to occur in South America. During the past 30 years a number of varieties reported to be resistant in experimental tests or in the field have been attacked by Midwestern races that had not been prevalent previously. Among these varieties are BUDA, BISON, WILLISTON GOLDEN, BOMBAY, VICTORY A, KOTO, and DAKOTA.

Whether these varieties succumbed to new races or to old races that had remained undetected is not known. Several races have been maintained as urediospore cultures for more than 20 years with no apparent change in pathogenicity. However, the chances of detecting changes towards greater virulence would require the identical mutation in each of the two nuclei of a urediospore. The possibility of detecting mutations for virulence is enhanced by the use of differentials with single rust-conditioning genes.

7. *Epidemiology*

From 1931 to 1951, inclusive, Flor (unpublished) determined the pathogenicity of 570 flax rust cultures secured from field collections. During these years BISON, KOTO, and DAKOTA, developed as rust-resistant varieties, were attacked by rust. Throughout the study, races carrying the least number of recessive (virulent) genes necessary for survival, *i.e.*, ability to attack a widely grown variety, predominated. With the passing years the percentage of cultures attacking differential varieties not grown commercially or experimentally decreased. Thus in the North Central States. where every rust-susceptible flax plant has the potential of playing the same role in the life cycle of the flax rust fungus that the barberry plays in the life cycle of the black stem rust fungus, there has been no tendency toward the development of races of virulence wider than necessary to attack commercial varieties.

8. New Rust-Resistant Lines

The 32 new and supplemental differential varieties listed in Table II have been backcrossed to BISON. In backcrossing, BISON is used as the female parent. All F_1 plants are heterozygous for the rust-conditioning gene of the male parent. In subsequent backcrosses the reaction of six to eight F_1 seedlings is determined first to a race of narrow virulence to which the male parent was susceptible and then to the race of widest virulence to which the male parent was resistant. All plants should be susceptible to the first race, and approximately half should be susceptible and half resistant, to the second. The susceptible plants lack a rust-resistant gene and are destroyed. The resistant plants are heterozygous for the desired gene and serve as the male parent for the next backcross to BISON. With this method two backcross generations may be grown in the greenhouse during the winter season at Fargo, North Dakota. From the progeny of the seventh backcross, lines are being selected that are pure for the desired rust-conditioning gene and have the agronomic type, wilt resistance, and pasmo tolerance of BISON. This reservoir of agronomically satisfactory lines should facilitate the development of new varieties of any desired rust-resistant genotype, within the limits of allelism.

9. Present Status and Future Trends

There appears to be no tendency toward the accumulation of virulent genes not necessary for survival in the races of flax rust predominating in the North Central States. On the contrary, surplus genes for virulence appear to diminish or disappear. If future studies verify these observations, it may be possible to control rust by a periodic and concerted shift to varieties or lines of a variety possessing different, or different combinations of, rust-conditioning genes.

Currently, the flax growing area of the North Central States is well supplied with rust-resistant varieties of flax. The flax breeder has a reservoir of 10 to 12 genes that condition resistance to all known North American races. However, in the recent past, BISON, KOTO. and DAKOTA, developed as rust-resistant varieties, have been so heavily damaged that they have nearly disappeared from cultivation. When or if our present varieties will be attacked is problematical. We know that all are susceptible to races occurring in South America. For the present we should exercise every precaution to exclude races of foreign origin and maintain a diversity in the rust-resistant germ plasm of our commercial flax varieties.

IV. THE PRESENT STATUS OF FLAX DISEASE OTHER THAN RUST

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1. General

In addition to rust, there are many other diseases of flax. A few of the more common ones are: wilt (*Fusarium lini* Bolley), pasmo (*Sphaerella linorum* Wllenw.), browning or stem break (*Polyspora lini* Laff.), seedling blight and root rot caused by species of fungi belonging to many genera (*Aphanomyces, Alternaria, Colletotrichum, Fusarium, Helminthosporium, Phoma, Pythium, Rhizoctonia, Thielavia,* and others), viruses (curly top and aster yellows), nonparasitic diseases, such as those caused by mineral deficiency, toxic substances, heat, and damaged seed. See Flor (1940), Millikan (1951), McKay (1947), Schuster and Anderson (1947), and Tervet (1937).

The importance of these diseases varies tremendously with climate, cultural practices, cropping sequence, and varieties grown. Some are destructive in one region but of no economic importance in another Thus, anthracnose is of minor importance in Australia, but for several years it was very destructive in California; in contrast, browning is of little importance in California, but it is of considerable importance in certain European Countries. Pasmo, as yet, is unknown in Mexico but it is a common disease in the upper Mississippi Valley. In regions where the precipitation is low, most foliage diseases like pasmo and anthracnose are not prevalent; whereas in regions of high precipitation, diseases of stems, leaves, bolls, and seed are not uncommon.

Wilt, pasmo, and anthracnose are usually considered the most destructive diseases. However, seedling blight and root rot of flax are often important diseases in many of the flax-growing regions. They are not conspicuous diseases, but they are sometimes as destructive as any of the so-called major diseases.

All the diseases mentioned in this manuscript have been described in textbooks or scientific journals and bulletins. Therefore, no attempt will be made to give their economic importance and distribution, describe their symptoms, or give the etiology of the pathogen. Attempts will be made to evaluate and bring together the more recent information on variability, physiologic specialization, varietal reaction, inheritance to disease, and diseases associated with damaged seed.

2. *Variability in Disease Reaction*

Temperature plays an important role in the development of any disease; this is especially true in relation to wilt of flax (Barker, 1923; Millikan, 1951; Houston and Knowles, 1953). Although temperature affects both the host and the pathogen, the effect apparently is much more important on the host. High temperature favors the growth of *Fusarium lini*, whereas it is rather detrimental to the development of the host.

Temperature also has a profound effect on the time of wilting of the host. Millikan (1951) in Australia, Kikuchi (1940) in Japan, Grossman (1934) in Germany, Wilson (1946) in Wales, and others maintain that the soil temperature is the limiting factor in the development of wilt. Tisdale (1917) found that the minimum temperature for wilting was about 15° C., whereas Tochinai (1925) gives the minimum as 10° C. Borlaug (1945) found that the minimum temperature for wilting differed with the race of *Fusarium lini* involved, and Kikuchi (1940) concluded that optimum temperature for wilt development differed with the variety concerned. Kommedahl and Christensen (1947) and others have shown that both seedling wilt and late wilt (at the time of flowering or beyond) occurred in the same variety, although the amount of wilting which occurred at a particular time was greatly influenced by temperature.

Varieties of flax, although resistant, may be induced to produce wilt under high temperature. All varieties of flax, whether susceptible or not, become infected with *Fusarium lini* but may not develop wilt unless exposed to high temperature (Schuster, 1944). Several investigators have demonstrated that susceptible varieties that normally wilt in the seedling stage can be prevented from wilting in that stage by growing the plants in a cool greenhouse. Similarly, late wilt can be induced by transferring plants grown in a cool house to a warm one. Millikan (1945) reported such changes could occur up to at least 20 weeks after germination. Therefore, in seasons when temperatures are high during the seedling stage, there is a tendency for seedling wilt to predominate. In other years when temperatures are high during the flowering stage of the plant and beyond, late wilt prevails.

It is rather significant that there is sometimes difficulty in distinguishing plants killed by late wilt from plants severely infected by pasmo or killed by root rot or those prematurely ripened by unfavorable climatic changes. As a consequence, late wilt is frequently overlooked. Obviously, this is of considerable importance in determining varietal reaction to diseases and in making genetic analyses.

3. *Physiologic Races*

Although physiologic specialization is a common characteristic in parasitic fungi, it has not been thoroughly investigated for the organisms that attack flax, with the possible exception of *Fusarium lini.* Differences in virulence of races are of paramount importance, because they greatly complicate the study of inheritance and selection of resistant varieties. The importance of physiologic specialization in *Fusarium lini* has been emphasized by several investigators. Borlaug (1945) demonstrated that *Fusarium lini* comprises many parasitic races or biotypes that differ greatly in their parasitic behavior on varieties of flax. Some races of *Fusarium lini* are highly virulent on some varieties of flax, others are moderately virulent, still others are only weakly virulent. One variety may be resistant to one race, but completely susceptible to another and vice versa. Millikan (1951) pointed out that certain varieties resistant in the United States were susceptible in Australia. Vanterpool (1944) also reported differences in resistance to wilt when the varieties were grown in different regions of Canada. *Fusarium lini* is one of the few species of *Fusarium* in which specificity in parasitism actually has been demonstrated. Apparently, there is no variety of flax that is resistant to all races of *Fusarium lini.*

Varieties of flax grown in the wilt nursery at St. Paul, Minnesota, over a period of years differ profoundly in their reaction to *Fusarium lini.* These changes apparently are caused by shifts in the population of races, because new races are periodically added to the wilt nursery. Then, when a new resistant variety is grown commercially, there is a gradual build-up of the population of races that can attack the hitherto resistant variety.

Borlaug (1945) also found marked antagonisms between races of *F. lini,* and concluded that, although there were many races present in the wilt nursery, there was a tendency for virulent races to be suppressed by nonvirulent races. Thus, the amount of wilt produced in a variety inoculated with a mixture of two races is much less than the amount produced by the same variety when inoculated with an individual race alone. His results indicated that varieties may be resistant in a wilt nursery infested with many races but completely susceptible when inoculated with individual races taken from that nursery.

Schwinghamer (1952) found that isolates of *Colletotrichum lini* obtained from Minnesota flax samples differed markedly from one another in cultural characters, in ability to produce appressoria, in penetration of the host, and in virulence on varieties of flax. Races were differentiated on the basis of the disease reaction of six varieties of flax.

Rodenhiser (1930) isolated several distinct cultural and parasitic races of *Sphaerella linorum*, and Sackston (1950) obtained differences between sporulating, highly pathogenic isolates and a nonsporulating, slightly pathogenic isolate. The writer also isolated many distinct cultural races, some of which differed in their relative virulence on varieties of flax. However, if a race was virulent on one variety, it was relatively virulent on other varieties; and similarly if a race was weakly pathogenic on one variety, the same relationship held for other varieties.

It is well known that *Rhizoctonia solani* comprises many physiologic races that differ greatly in their parasitic ability on flax and other crops. Similarly, *Polyspora lini* comprises many cultural races, and additional studies may reveal parasitic races.

4. Varietal Resistance

It has been known for a long time that varieties of flax differ greatly in their susceptibility and resistance to disease (Barker, 1923; Borlaug, 1945). The reaction of current varieties to wilt and pasmo are given by Culbertson *et al.* (1952). Before the development of wilt-resistant varieties, wilt was the limiting factor in flax production on land that had previously grown flax. During the past 20 years, the writer, in cooperation with the Department of Agronomy and Plant Genetics and the United States Department of Agriculture, has tested for wilt resistance thousands of lines and varieties of flax which were obtained from many different sources in North America and other countries. Most varieties were susceptible to wilt, a small percentage were resistant, others were intermediate in their reaction. Many of the susceptible varieties, however, have resistant genotypes that usually remain resistant in additional tests. Recently Knowles and Houston (1953) reported similar results. This method of selecting resistant varieties from heterogeneous varieties has long been recognized, and it also has been used by many investigators in developing other crops resistant to *Fusarium* wilt.

These varietal tests are made in wilt-sick soil in a "Disease Garden" —a plot of land on which varieties of flax are grown in successive years and subjected to the most severe wilt tests that can be devised. The soil in these gardens is inoculated with all available physiologic races of *F. lini*, and from time to time infested flax material from diverse sources is added to the garden. It is actually a test of the survival of the fittest, because all wilt-susceptible varieties are eliminated. Because of the ease of making these tests, many resistant varieties of diverse genotypes have been developed. Therefore, if it were not for the introduction or development of new parasitic races of *Fusarium lini*, the wilt problem would be of little importance today.

Varietal resistance also has been reported for several other diseases. In recent years, extensive varietal tests for resistance to pasmo have been made in the United States and Canada. At Minnesota, many thousands of varieties and lines have been artificially inoculated with many isolates of the pasmo organism. None were resistant, although some were much less susceptible than others. Varieties like BOLLEY GOLDEN (C. I. 644), RIO (C I. 280), and VICTORY (C. I. 1045) were very susceptible, whereas CRYSTAL (C. I. 982), BISON (C. I. 389), and C. I. 975 were among the more resistant ones and are usually designated as moderately susceptible or moderately resistant. Genes for the more resistant characters are now being incorporated into new improved varieties.

Since seedling blights and root rots are caused by many pathogens, obviously it is rather difficult to obtain varieties that are resistant to this complex. Nevertheless varieties do differ in resistance to specific organisms. Ray (1945) made a very extensive study of varietal reaction to *Colletotrichum lini*. He found marked differences in susceptibility and reported PUNJAB very susceptible; whereas LINOTA and a selection of BUDA were very resistant. Schwinghamer (1952) obtained similar results. Colhoun (1948) reported HINDI and LA PLATA resistant to *Phoma*. Tsiang (1947) concluded that REDWING (C. I. 320) was more resistant to *Rhizoctonia* than the other 48 varieties tested.

5. *Nature of Inheritance*

The number of factors conditioning resistance in flax to *Fusarium lini* is difficult to determine, because resistance to wilt is only relative and varietal reaction can be influenced profoundly by temperature and also altered greatly by changes in population of races. Many workers have made crosses between resistant and susceptible varieties and obtained resistant progenies, but only a few have made studies on inheritance to wilt. Allison and Christensen (1938) found that the F_1 hybrids were intermediate between the two parents. The segregation ratio obtained in F_2 and advanced generations indicated that several factors were involved. This is in accord with the findings of Tisdale (1917) and Burnham (1932). Variability in segregation ratios is to be expected, because there appears to be an indefinite number of biotypes of *Fusarium lini* that have virtually imperceptible differences in virulence on a variety. Studies at Minnesota also indicate that the reaction of the F_1 hybrids can readily be shifted from an intermediate reaction to susceptibility or resistance by a slight change in temperature, and this greatly complicates genetic studies on disease resistance. Because of the tremendous genetic variation in the pathogens, studies on inheritance of reaction to *F. lini* should preferably involve known races of the organism.

As yet, no extensive genetic studies have been made on the inheritance of resistance to stem break, anthracnose, pasmo, and root rots.

6. Seed Damage in Relation to Germination, Stand, and Yield

Recent studies have emphasized the importance of damaged flax seeds because they often are responsible, directly or indirectly, for poor stands and lower yields (Machacek and Brown, 1945); Forsyth and Vogel, 1945; Moore and Christensen, 1946; Machacek and Greaney, 1948; Kommedahl and Christensen, 1950; Kommedahl *et al.*, 1950. There are at least three types of seed damage that commonly contribute to poor field performance. The most common is the cracking, splitting, and chipping of the seed coat resulting from harvesting and threshing, especially during dry weather.

At Minnesota, hundreds of seed lots have been examined and in certain years a high percentage was found to be severely damaged; 30 to 50 per cent was not uncommon and occasionally virtually every seed had some type of injury. Similar results have been reported at other institutions.

In addition to the external injury, there may be varying degrees of internal injury not apparent until the seed germinates. Frequently, the root tip is broken off, sometimes it is split or cracked; and sometimes the cotyledons are injured in different ways.

Another type of damage is a natural split in the edge of the seed coat at the smaller end of the seed. In this case the seed coat curls back, creating an opening not unlike a fish mouth (Fig. 3). This difficulty is not caused by mistreatment, but it appears to be due to weather and soil factors, because it occurs while the seed is still in the boll. There may be tremendous variations in percentage of this damage in the same varieties when grown in different regions of the United States or in the same region in different years. This kind of injury is especially common in yellow-seeded varieties, but it is usually of little importance in brown-seeded varieties. Varieties like CRYSTAL and BOLLEY GOLDEN may have as much as 50 to 70 per cent of this type of damaged seed. Lots with 10 to 30 per cent are not uncommon.

The third type of damage is the blighting of seed caused by many species of fungi. In many regions of the world, particularly in the more humid regions, microorganisms are very common on seed; whereas the seeds are relatively free of fungi in the arid regions. Species belonging to many genera have been isolated from flax seed; and under certain conditions, they may cause pre-emergence killing and seedling blight. *Alternaria* usually predominates, but the species commonly encountered are weakly pathogenic. *Colletotrichum lini* and *Fusarium* spp. are the most common root-rotting pathogens on the seed. In the Midwest, seed with 50 to 75 per cent *Alternaria* infection is not uncommon, and in certain years a high percentage of seed also may be infected with *Colletotrichum*, occasionally more than 50 per cent. Such seed is frequently the source of primary infection of seedling blight.

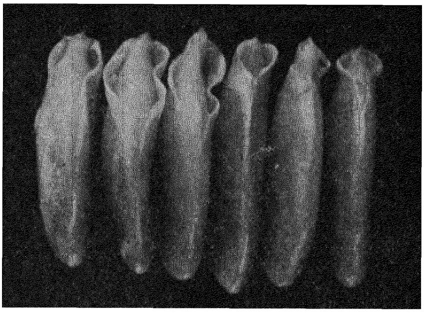

FIG. 3. Natural split of flaxseed coat through which soil-inhabiting fungi may enter and rot the seed before it germinates.

The percentage of germination from naturally and mechanically injured seed is usually much inferior to that of sound seed, whereas *Alternaria* infection seldom reduces germination. It is rather significant that mechanically damaged seed sometimes germinates well on blotters, but very poorly when planted in the soil. Sometimes there is more than a 50 per cent difference in germination. The openings and cracks in the seed coats, although frequently so small as to be visible only with the use of a good magnifying glass, serve as an entrance for many species of fungi. Therefore, when such seeds are planted under conditions favorable for germination, soil-inhabiting fungi may enter through the minute breaks and infect the seed before it germinates and also may rot the seed, causing pre-emergence killing. Much of the seed rot and seedling blight associated with damaged seed can be prevented by seed treatment.

Chemical seed treatment places a protective layer of fungicide over the openings and prevents the entrance of seed-rotting organisms. Appropriate treatment also will destroy the pathogens on the seed—*e.g.*, *Fusarium*, *Colletotrichum*, and *Polyspora*. Over a period of years, thousands of samples have been tested at St. Paul. About three out of four responded favorably to seed treatment. However, an increase in stand was not necessarily followed by an equal increase in yield. Seed treatment may actually double or triple the stand, particularly when samples have a high percentage of damaged seed. The value of seed treatment, however, varies tremendously, not only with the seed lot but also with the region where the flax is sown. In many parts of the world seed treatment is distinctly beneficial, whereas in other regions it may be of little value. In general, tests indicate that the more extensive the seed coat injuries, the greater the need for seed treatment, and the greater the benefit from it. Recent investigations have shown clearly that a higher rate of treatment should be used for flax than is used in treating cereals. Thus, New Improved Ceresan should be used at the rate of 1½ ounce per bushel. Seed treatment will not control wilt.

For additional information and references on flax disease, the readers are referred to Millikan's comprehensive publication on "Diseases of Flax and Linseed," 1951.

V. Weeds

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1. General

Weed control is especially important in the flax crop. Not only do weeds reduce yields of flaxseed and depreciate its value for oil but they also interfere seriously in the utilization of the straw. The flax plant is a poor competitor. The erect slender stems that branch near the top to form the inflorescence, the small simple leaves, and the relatively short growth make it an excellent companion crop for small-seeded legumes and grasses and a poor control crop for weeds. Burrows and Olson (1952) have shown that 10 wild mustard, *Brassica kaber*, plants per square yard in a good stand of flax reduced the yield of seed 63 per cent; 50 plants caused a 73.4 per cent reduction; and 100 plants an 85.5 per cent loss when compared to weed-free flax. In unpublished data Stoa reports a 38 per cent reduction in yield of seed as an average of six station years in North Dakota from competition of *Setaria viridis* and *S. glauca* with flax. Robinson (1949) found that weeds less than 6 in. tall provided most of the competition for oats and wheat but those over 6 in. were more responsible for reduced yield of flax seed.

In spite of its natural inability to compete with weeds satisfactorily, flax has become potentially one of the "cleanest" drill-sown crops.

Largely, this has been a recent accomplishment through advances in the methods of chemical control.

2. *Chemical Control*

a. Effect of Herbicides on Weeds. On the flax-growing acreage of the North Central States and Montana, MCP (amine salt of 2-methyl-4-chlorophenoxyacetic acid), 2,4–D (amine salts and esters of 2,4-dichlorophenoxyacetic acid), and TCA (sodium salt of trichloroacetic acid) are used satisfactorily to control the annual weeds common to this area with the exception of wild oats, *Avena fatua,* wild buckwheat, *Polygonum convolvulus,* and smartweed, *Polygonum pennsylvanicum* and *P. persicaria,* which cannot be removed selectively with these herbicides. Swift (1949), however, reports successful removal of wild oats from flax with IPC (Isopropyl-*N*-phenyl carbamate) in California.

Perennial weeds are not successfully controlled by post-emergence applications of these herbicides, since the amounts required injure flax. Troublesome annual weeds are both monocotyledons and dicotyledons. Wild mustard, *Brassica kaber,* lamb-quarters, *Chenopodium album,* ragweed, *Ambrosia artemisifolia,* and rough pigweed, *Amaranthus retroflexus,* are among the more common broad-leaved species found in the North Central States, and foxtail, *Setaria viridis* and *S. glauca,* barnyard grass, *Echinochloa crusgalli,* and wild oats, *Avena fatua,* are the most common grass weeds. With the exception of wild oats, the grass weeds are successfully controlled with 5 to 7 pounds of TCA, acid equivalent, per acre applied when the weeds are less than 3 in. tall. The broad-leaved weeds are controlled with 3 to 4 oz. of MCP or 2,4–D, acid equivalent per acre. MCP is preferred because, as Blackman (1952), Mullison (1951), Templeman and Halliday (1950) and Dunham (1952a, b) have shown, it is less injurious to the crop. Although 2,4–D kills some species that are tolerant of MCP and vice versa, as reported by Dunham *et al.* (1952), there is no practical difference in the reaction of weeds common in flax to these herbicides except for pigweed, which is more susceptible to 2,4–D. Wiese (1953), working in Minnesota, was unable to control wild oats selectively in flax with IPC or CIPC (Isopropyl *N*-(3-chlorophenyl) carbamate) because of injury to the crop. He applied the chemical the fall preceding sowing of flax, in the spring preceding sowing, and post-emergence.

b. Effect of Herbicides on Flax. In selective spraying, the effect on the crop is of at least equal importance to that on the weeds. Flax is less tolerant of 2,4–D and MCP than are the small grains. In experiments with weed-free flax at the Minnesota Agricultural Experiment Station, the yield was reduced in proportion to the amount of sands of samples have been tested at St. Paul. About three out of four responded favorably to seed treatment. However, an increase in stand was not necessarily followed by an equal increase in yield. Seed treatment may actually double or triple the stand, particularly when samples have a high percentage of damaged seed. The value of seed treatment, however, varies tremendously, not only with the seed lot but also with the region where the flax is sown. In many parts of the world seed treatment is distinctly beneficial, whereas in other regions it may be of little value. In general, tests indicate that the more extensive the seed coat injuries, the greater the need for seed treatment, and the greater the benefit from it. Recent investigations have shown clearly that a higher rate of treatment should be used for flax than is used in treating cereals. Thus, New Improved Ceresan should be used at the rate of 1½ ounce per bushel. Seed treatment will not control wilt.

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2,4–D, MCP, or TCA spray applied. When mustard was present in the crop, the yield of flax was increased by spraying with recommended amounts of 2,4–D, because the competition of the mustard was more injurious than the 2,4–D. Amounts that are too large have reduced the yield of flax even when the weeds were killed. The use of 2,4–D, MCP, or TCA for weed control in flax is advisable only when the loss from weeds is expected to be greater than that from the spray. Among the farm crops, flax is more tolerant of TCA than corn, oats, wheat, barley, or soybeans.

Susceptibility to herbicides may be measured by (1) abnormalities induced by treatment, (2) effect on maturity date, (3) decrease in yield of seed, (4) change in quality, and (5) effect on annually sprayed progeny. Susceptibility is affected by variety, environmental conditions, and the kind of herbicide. Varietal differences in reaction of flax to 2,4–D as expressed in several characters were shown by Tandon in 1948. Numerous investigators have confirmed his finding, as measured by yield, in later studies reported in the Sixth Annual Research Report of the North Central Weed Control Conference. Evidence is available from a study by Bothun (1953) at Minnesota that varietal response is genetically controlled and can be transmitted according to the laws of heredity. Environment is a factor not well understood. Paatela (1949) associated differential response with rate of growth and concluded that variations in resistance at different times of application may be negatively associated with variations in the natural auxin content of the flax plant. Shulstad (1950) found that in bimonthly sowings of seven varieties of flax from May to July, the order of tolerance varied with dates of sowing. REDWING, which was the most tolerant variety if sown early, became susceptible in later sowings. Flax is more tolerant of MCP than of 2,4–D, and, among the formulations of 2,4–D, it is more tolerant of the sodium and amine salts than the esters. Varietal differences are less important when MCP is used instead of 2,4–D and when the salts of 2,4–D are used instead of the esters.

(*1*) *Abnormalities.* The common abnormalities that result from 2,4–D are stem curvature, "fused" leaves (bi-lobed), fused bolls, and fasciated stems. They are found in unsprayed plants, but the frequency of occurrence is increased by 2,4–D. The first external change in plants is drooping or bending which begins within a couple of hours after spraying. These plants later straighten and regain a normal appearance unless they are very susceptible varieties or were sprayed with excessive dosages. Sharma (1950) found that the number of days required for recovery varied with the stage at which the flax was treated. There was no recovery of the varieties he worked with (REDWING, DAKOTA, and MINERVA) when sprayed at full bloom; at earlier stages the period of recovery varied from 3 to 7½ days. He also found that the region of abnormality was higher on the plant as the stage of development at time of spraying progressed, indicating probably, that there was a certain delicate region in the terminal bud which was affected by the chemical and that it moved up as the plant developed. Flax sprayed with recommended rates of MCP has not shown these abnormalities except in initial temporary bending. No such responses have been observed as a result of spraying with TCA, although dieback, crinkling, and burning of the leaves sometimes happens.

(2) *Maturity.* The response of flax to herbicides may be manifested in delayed maturity. Frequently blooming dates are delayed much longer than dates of ripening, since Tandon (1949), Paatela (1949), and Sharma (1950) have all shown that the rate of elongation of flax sprayed with 2,4–D was greater than the check after the initial shock had been overcome. When tolerant varieties have been sprayed at recommended rates of 2,4–D and prior to the bud stage, Tandon (1949) and Sharma (1950) found dates of ripening to be delayed by only 1 or 2 days. In some seasons, flax becomes indeterminate in growth and full maturity may not be reached at all, but, under these conditions, unsprayed and sprayed plants behaved alike. Shulstad (1950) found, however, that relative delay in ripening was affected by variety and date of sowing. Thus, MINERVA sown April 27 was delayed 1 day by 4 oz. of 2,4–D but 17 days when sown June 10. REDWING sown April 27 was delayed 2 days and only 3 days when sown June 10.

Delay from MCP has been less than from 2,4–D, and delay from TCA at 7 pounds per acre has occurred only from spraying during a 10- to 12-day period after emergence.

(3) *Yield.* Although morphological responses indicate relative susceptibility to 2,4–D, they are not closely correlated with yield except when spraying is done during blooming. Dunham (1952b), Foster (1949), Friesen (1949), Friesen and Olson (1951), Leggett (1950), and Sexsmith (1950) have studied flax response to time of spraying. In general, spraying from early bud stage through full bloom has been hazardous. It has been difficult to discover any pattern at earlier stages. Dunham (1952b) states that: "As a result of trials for three years with one variety and for two years with three varieties, spraying separate weed-free plots every other day from emergence until full bloom has shown that response to time of spraying varies with years." In the original study by Dunham and Robinson (unpublished) no association between reduction in yield and rate of growth at time of spraying as measured by increase in height could be discovered. In similar trials at

Minnesota, REDWOOD flax showed maximum reduction in yield when sprayed with 7 pounds of TCA during the first 12 days after emergence.

(*4*) *Quality*. The percentage of oil and its iodine number may also be affected by the use of herbicides. Apparently, however, there are other factors which make it difficult to discover the relation of 2,4–D to these attributes of quality. In Tandon's study (Tandon, 1949), the ester reduced both the oil content and the iodine number in 6 out of 7 varieties. In subsequent studies at Minnesota, the per cent of oil has been reduced in 25 out of 64 comparisons by amines and in 19 out of 47 comparisons by the ester. The iodine number has been lowered in 32 out of 64 comparisons by the amine and in 28 out of 47 by the ester. Shulstad (1950) made oil and iodine-number determinations for 5 varieties of flax sown at 7 successive dates, and sprayed with 8 oz. of a micronized 2,4–D acid per acre. He found no significant changes in either oil per cent or iodine number as a result of spraying.

Paatela (1949) reported a consistent reduction in oil per cent using the sodium salt of 2,4-D. Heggeness and Le Tourneau (1949) showed a 5 per cent reduction in oil when flax was sprayed in the bud stage. Friesen (1949) found no reduction in oil or iodine number in one year and a small lowering of the iodine number in another season. Chubb and Mac Key (1949) reported no reduction in oil content or iodine number with less than 8 oz. of amine per acre in two years of trial.

Klosterman and Clagett (1949) considered the differences in oil content between sprayed and unsprayed fields of three varieties to be small. The iodine number of oil from MINERVA, however, was significantly reduced by spraying.

(5) *Annually Sprayed Progeny*. There has been considerable speculation as to the effect on flax grown from seed harvested from plants sprayed with 2,4–D and also as to whether plants sprayed through several generations might develop either more or less tolerance to the herbicide. In studies at Minnesota the flax grown from seed of plants sprayed the year before at four stages of growth with three rates each of sodium salt, amine salt, and ester of 2,4–D showed no difference from flax grown from unsprayed plants. Data studied were yields of seed and straw, number of basal branches per plant, stem curvature, number of fasciated stems, and excessive branching of the inflorescence. In an attempt to answer the second question, progenies of flax sprayed each year through four generations and progenies of flax never sprayed have been maintained in Minnesota. Spraying both progenies with 2,4–D in the test year has shown no visible change in plant characters due to this continued treatment nor has the sprayed progeny shown any accumulated tolerance or susceptibility to the herbicide.

3. *Cultural Methods*

(*a*) *Crop Sequence.* Control of weeds by cultural practices is important for the economical production of flax. The proper sequence of crops plus effective cultivation can reduce the weed seed population of a soil layer so that a succeeding flax crop will be relatively free from annual weeds. Two studies at Minnesota contribute information relative to this practice. The effect of growing different crops given normal cultural care on soil of known weed seed content was determined in a succeeding crop of flax. In the first experiment weed seeds were drilled into all plots at the beginning of the trial, soil was sampled to 7 in., and weed seeds in this layer were counted. Sampling and counting was repeated in the flax following two years of growing each crop on the same plot. Yields of flax and dry weights of weeds also were obtained. The following crops were compared: corn, soybeans, alfalfa, Sudan grass, winter wheat, oats, and oats undersown to alfalfa. The winter wheat was preceded by a summer fallow, the oats stubble was disked to stimulate germination of weed seeds, and the alfalfa was mowed after oats harvest in one case and left unmowed in the other. A complete summer fallow was also included. Except where cultivation accompanied the cropping, the weed seed population of the soil increased from 100 to 312 per cent. Even when fall mowing was practiced, the weed seeds increased in number. In contrast, the largest reduction in weed seeds occurred following fallow, fallow plus winter wheat, and disked oats stubble. Cultivation apparently stimulated germination, as shown by the fact that the largest weights of weeds in the flax crop also followed cultivated crops and fallow.

(*b*) *Tillage Practices.* In the second experiment, tillage practices have been compared in two rotations: (1) alfalfa-alfalfa-corn-flax and (2) clover and timothy-corn-oats-flax. In the first rotation, corn kept free from weeds by normal cultivation plus hoeing, was compared with corn given only normal cultivation. In the second rotation, oats stubble plowed in August was compared with oats stubble disked in August and oats stubble plowed in September. In both rotations the seedbed for flax was prepared by shallow cultivation in the spring following each cultural practice of the preceding fall. Data in both experiments consisted of counts of weed seeds in the soil and yields of flax and dry weights of weeds. After one rotation cycle, the original weed seed population was reduced 40 per cent by hoed corn, 20 per cent by oats stubble plowed in August, 35 per cent by oats stubble disked in August, and 9 per cent by oats stubble plowed in September. In the second flax crop of the rotations, there were fewest weeds following hoed corn and disked oats stubble. Application of TCA and 2,4-D at the last corn cultivation controls late germinating annual weeds and is a practical substitute for hoeing.

(*c*) *Rates and Distribution of Seed.* The effectiveness of heavy stands on weed control in flax also has been investigated in Minnesota. Increasing the rate of sowing above that recommended for general farm practice has given neither better weed control nor better yields of seed or straw. In a study of seed distribution, flax was sown (1) in drill rows spaced 6 in. apart compared to 7 in. and (2) sown in one direction compared to cross-sowing. The 6-in. spacing resulted in significantly better weed control and when rate of sowing per acre for 7-in. spacing was reduced to $\frac{6}{7}$ of the rate used for 6-in. spacing, the yield was also significantly higher for the 6-in. spacing. With an early variety, weed control was better when 56 pounds of flax seed were sown in two directions—28 pounds one way and 28 pounds at right angles—than when sown in one direction, but did not result in a higher yield. There was no advantage in cross-sowing a late variety.

VI. BREEDING

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1. *General*

Although hybridization was practiced prior to 1936, all of the varieties then recommended had been developed by selection rather than by hybridization. With the exception of a few varieties such as REDWING in Minnesota and PUNJAB in California, all the varieties recommended in 1953 were developed by hybridization.

Since linseed oil is the most valuable product obtained from seed-flax, the ultimate objective must be the production of high yield of high quality oil per acre. High oil yield depends upon both high seed yield and a high percentage of oil in the seed. Data reported by Culbertson (1949) show a high correlation between seed yield and oil yield per acre, indicating the relatively great importance of high seed yield.

The ability of a variety to produce a high yield of seed depends upon the favorable association of a number of characters such as disease resistance, suitable agronomic type, and inherent yielding ability.

2. *Methods of Breeding*

The pedigree method has been used most widely in developing improved flax varieties, although other methods such as the backcross, multiple cross, or bulk methods may be used in some cases (Hayes and Immer, 1942). The pedigree method now used at the Minnesota Agricultural Experiment Station consists of (1) making a cross between two parents that together possess the characters to be combined in a new variety: (2) growing the progenies of selected plants in space planted rows so that individual plants may be observed; and (3) keeping a record so that the individual plant may be traced from one generation to the next. Steps included in this method are outlined as follows:

1st year: The cross is made in the field, and the F_1 plants are grown in the greenhouse.

2nd year: From 2000 to 10,000 F_2 plants are grown in space-planted rows on wilt-infected soil. Plants are selected from this population that combine the desired agronomic characters, resistance to wilt and to any other diseases that may be present. The seed is observed, and any selections with small or inferior seed are discarded. About 25 seedlings from each surviving selection grown in a 4-in. pot in the greenhouse are inoculated with rust spores when about 3 to 4 in. high. Only lines breeding true for rust resistance are retained. Seed of these rust-resistant lines is then tested for oil quality, and only the best lines are saved. Rust-resistant plants of those lines having high oil quality may be grown to maturity in the greenhouse, thus completing the third generation.

3rd year: F_4 plants are grown in space-planted rows on wilt-infected soil, and selection similar to that practiced in F_2 is followed. Tests for rust resistance and oil quality are made in the manner described above.

4th year: F_5 plants are grown in the field on wilt-sick soil. During the summer the rows are observed for uniformity as well as desirable agronomic characters, resistance to wilt and other diseases. Those rows that appear uniform and have the desired agronomic type are harvested in bulk, given a final test for rust resistance and oil quality, and, if sufficient seed is available, are tested for oil content.

5th year: Lines developed in this way are placed in preliminary yield trials.

3. *Inheritance of Characters*

a. Plant Height. It has been shown that the inheritance of plant height is governed by multiple factors. In the study of the cross, BISON

× TALMUNE, Moseman (1944) found no indication of dominance of either tall or short stature. Chu and Culbertson (1952) found a slight tendency for phenotypic dominance of tall stature in a cross of DAKOTA × Indian 1193-2. Carnahan (1947) studied the combining ability of four desirable flax varieties with four tester varieties and found in most cases the mean heights of both the F_1 and F_2 generations were slightly greater than the mean of the two parents, although the differences were small and statistically nonsignificant. Transgressive segregation for height has been noted at the Minnesota Agricultural Experiment Station, where true-breeding lines selected from the cross, BIWING × B5128, were 5 in. taller than the average of the parents. It seems probable that types shorter than the parents could be selected as easily as taller types, but shorter types usually are discarded as undesirable.

b. Seed Size. Myers (1936) found evidence of not more than three factor pairs governing the inheritance of seed size in his study of the F_2 of a cross of REDWING × Ottawa 770B. Moseman (1944) reported the inheritance of seed size to be due to a small number of multiple factors, since he was able to recover the parental types among the F_4 generation. Chu (1949) reported that not less than four major factor pairs were responsible for the inheritance of seed size in his material.

c. Seed Yield. Moseman (1944) pointed out that selection for high seed yield based upon the yields of individual plants would be of little value because of the wide range in variation of the individual plants due to environmental influences. In a study of the F_1 and F_2 generations of 16 crosses, Carnahan (1947) found the mean yield of F_1 and F_2 exceeded the mean of the parents by 40 and 27 per cent, respectively. In a further study (1949) he found that 84 out of 117 F_3 lines exceeded the yield of the higher yielding parent, 33 by a significant amount. Heterosis is demonstrated by the fact that the mean seed yield of all F_3 lines exceeded the mean yield of the parents by 16 per cent.

d. Oil Percentage. The inheritance of oil percentage appears to be governed by multiple factors, as evidenced by the fact that a considerable variation in oil percentage occurs in a series of varieties. Carnahan (1949) studied the progenies of a cross between DAKOTA with brown seeds and low oil content by MINERVA with yellow seeds of unusually high oil content, and found that oil percentage was governed by a major factor pair and minor modifying factors. It was not proved that the major factor pair expression for oil content was other than the result of a physiological association between seed color and oil content, since the yellow seeded segregates had a significantly higher oil percentage than the brown-seeded segregates.

e. Iodine Numbers. Iodine number of the oil apparently is inherited on a multiple-factor basis. In the cross of DAKOTA × MINERVA, Carnahan (1949) found evidence of a major factor pair determining seed color and other inherited factors that influenced iodine number.

f. Resistance to Herbicides. Recently there has been considerable interest in the response of flax varieties to various herbicides, and many references can be found in the literature listing the relative susceptibility of various varieties. Bothun (1953) studied the inheritance of reaction to 2,4–D of the parents, backcrosses of the F_1 to both parents, F_1, F_2, and F_3 generations in three crosses, CRYSTAL × B5128, B5128 × REDWING, and REDWING × CRYSTAL. Stem curvature was found to be simply inherited with phenotypic dominance lacking. The factors in B5128 and CRYSTAL conditioning this character appeared similar. Early recovery from stem curvature apparently was inherited as a phenotypic dominant in the crosses involving REDWING. Phenotypic dominance of earlier first, full, and last bloom was absent in CRYSTAL × REDWING, partial in B5128 × REDWING, and complete in CRYSTAL × B5128.

Phenotypic dominance was complete for a greater percentage of plants with fused leaves in B5128 × REDWING; complete for a smaller number of plants with fused leaves in CRYSTAL and B5128; and lacking in CRYSTAL × REDWING. Bothun (1953) concluded that it would be possible to breed flax varieties tolerant to 2,4–D and perhaps to other herbicides as well.

4. Cytologic Studies

The best known of the 10 genera comprising the flax family, *Linacere,* is the genus, *Linum,* composed of approximately 100 species. Commercial flax is of the species *Linum usitatissimum.* Interspecific crosses have been attempted without much success except between *L. usitatissimum* and *L. angustifolium.*

Ray (1944) studied cytologically the chromosomes of 86 collections of the genus *Linum,* including 30 species, and 28 commercial varieties of commercial flax *L. usitatissimum,* with particular reference to number, size, and shape. He has listed his results together with that of previous workers wherever possible. The chromosome number in all commercial varieties was found to be $N = 15$. Ray recognized five haploid numbers: 8, 9, 10, 14, and 15. In addition, earlier workers had reported finding haploid numbers of 12, 16, and 18. Three different groups were noted as determined by chromosome size. When size and number of chromosomes was considered, seven karyotypes were recognized.

The most common chromosome number was $N = 9$, with $N = 15$ next most common.

5. *Varieties*

The number of flax varieties developed in the United States has been relatively small, and only a few have been grown at any one time. Dillman (1953) reported the results of his studies of the classification of flax varieties up to 1946, and the reader is referred to his work for a full description of each variety. A few varieties released since 1946 should be mentioned briefly.

MARINE was developed at the North Dakota Agricultural Experiment Station from a cross of C. I. 975 × SHEYENNE. It is an early variety resistant to wilt, immune to North American races of rust, and as tolerant to pasmo as any commercial variety. REDWOOD, developed at the Minnesota Agricultural Experiment Station, is mid-late variety, moderately resistant to wilt, immune to North American races of rust, but moderately susceptible to pasmo. These varieties have been described more fully in the *Agronomy Journal* by Culbertson (1952, 1953).

PUNJAB 47 and IMPERIAL were developed by the California Agricultural Experiment Station by selection from PUNJAB (C. I. 20). Both are similar to PUNJAB, but have higher yielding ability. All the PUNJAB varieties are susceptible to wilt and pasmo, but resistant to many races of rust found in North America.

6. *Problems of the Future*

Because of the changing nature of the pathogens attacking flax, plant breeders must be constantly alert to retain the progress made in breeding varieties resistant to both wilt and rust. A further search for a source of resistance to pasmo is highly desirable. Minor diseases not recognized at present as being of a serious nature may become relatively more important, so that it may be necessary to breed for resistance to other diseases. The increasing use of herbicides on flax for the control of weeds presents a problem in breeding varieties tolerant to the current herbicides. Improved varieties of the future should combine higher oil content and oil quality with these other desirable characters.

REFERENCES

Storage Properties of Flaxseed

Altschul, A. M., Karon, M. L., Kyame, Lillian, and Hall, Catherine M. 1946. *Plant Physiol.* **21**, 573–587.

Bailey, C. H. 1940. *Plant Physiol.* **15**, 257–274.

Barton-Wright, E. C., and Tomkins, R. G. 1940. *Cereal Chem.* **17,** 332–342.

Bottomley, R. A., Christensen, C. M., and Geddes, W. F. 1950. *Cereal Chem.* **27,** 271–296.

Coleman, D. A., and Fellows, H. C. 1925. *Cereal Chem.* **2,** 275–287.

Galloway, L. D. 1935. *J. Textile Inst.* (*Trans.*) **26,** T123–129.

Gilman, J. C., and Barron, D. H. 1930. *Plant Physiol.* **5,** 565–573.

Gilman, J. C., and Semeniuk, G. 1948. *Trans. Am. Assoc. Cereal Chemists* **6,** 108–112.

Haines, R. B. 1937. *Dept. Sci. Ind. Research* (*Brit.*). *Food Invest. Special Rept. No.* **45.**

Karon, M. L., and Adams, Mabelle E. 1949. *Cereal Chem.* **26,** 1–12.

Koehler, B. 1938. *J. Agr. Research* **56,** 291–307.

Larmour, R. K., Clayton, J. S., and Wrenshall, C. L. 1935. *Can. J. Research* **12,** 627–645.

Larmour, R. K., Sallans, H. R., and Craig, B. M. 1944. *Can. J. Research* **F22,** 9–18.

Lea, C. H. 1933. *J. Soc. Chem. Ind.* (*London*) **52,** 57–63.

Leach, W. 1944. *Can. J. Research* **C22,** 150–161.

Macara, T. J. R. 1943. *J. Soc. Chem. Ind.* (*London*) **62,** 104–106.

Matz, S. A., and Milner, M. 1951. *Cereal Chem.* **28,** 196–207.

Milner, M. 1946. *Science* **104,** 463–464.

Milner, M., Christensen, C. M., and Geddes, W. F. 1947a. *Cereal Chem.* **24,** 182–199.

Milner, M., Christensen, C. M., and Geddes, W. F. 1947b. *Cereal Chem.* **24,** 507–517.

Milner, M., and Geddes, W. F. 1945. *Cereal Chem.* **22,** 484–501.

Milner, M., and Geddes, W. F. 1946. *Cereal Chem.* **23,** 449–470.

Mukherjee, S. 1952. *Arch. Biochem. and Biophys.* **36,** 23–59.

Nagel, C. M., and Semeniuk, G. 1947. *Plant Physiol.* **22,** 20–33.

Oxley, T. A. 1948. "The Scientific Principles of Grain Storage." Northern Publishing Co., Liverpool. See Chapter II, pp. 7–15.

Ramstad, P. E., and Geddes, W. F. 1942. *Minnesota Agr. Expt. Sta. Tech. Bull.* **156.**

Schricker, J. A. 1948. M.S. Thesis, University of Minnesota, St. Paul.

Semeniuk, G., Nagel, C. M., and Gilman, J. C. 1947. *Iowa State Agr. Expt. Sta. Research Bull.* **349.**

Smith, G. 1938. "An Introduction to Industrial Mycology." Edward Arnold and Company, London.

Snow, D., Crichton, M. H. G., and Wright, N. C. 1944. *Ann. Applied Biol.* **31,** 102–110.

Vayssière, P. 1948. "Preservation of Grains in Storage," pp. 115–122. Food and Agriculture Organization of the United Nations, Washington, D. C.

Zeleny, L. 1940. *Cereal Chem,* **17,** 29–37.

Zeleny, L. 1948. *Trans. Am. Assoc. Cereal Chemists* **6,** 112–125.

Rust

Cruickshank, I. A. M. 1952. *New Zealand J. Sci. Technol.* **B34,** 128–133.

Dillman, A. C. 1953. *U. S. Dept. Agr. Tech. Bull.* **1064.**

Flor, H. H. 1935. *J. Agr. Research* **51,** 819–837.

Flor, H. H. 1940. *J. Agr. Research* **60,** 575–591.

Flor, H. H. 1941. *Phytopathology* **31,** 852–854.

Flor, H. H. 1942. *Phytopathology* **32,** 653–669.

Flor, H. H. 1946. *J. Agr. Research* **73,** 335–357.

Flor, H. H. 1947. *J. Agr. Research* **74,** 241–262.

Henry, A. W. 1930. *Phytopathology* **20**, 707–721.
Kerr, H. B. 1952. *Nature* **169**, 159.
Myers, W. M. 1937, *J. Agr. Research* **55**, 631–666.
Prasada, R. 1948. *Indian Phytopathology* **1**, 1–18.
Straib, W. 1939a. *Nachrbl. deut. Pflanzenschutzdienst* **19**, 49–51.
Straib, W. 1939b. *Züchter* **11**, 130–136, 162–168.
Vallega, J. 1938. *Revista argentina agron.* **5** (1), 25–56.
Vallega, J. 1944. *Santa Catalina Inst. Fitotéc. An.* **4**, 59–74.
Waterhouse, W. L., and Watson, I. A. 1941. *J. Proc. Roy. Soc. N. S. Wales.* **75**, 115–117.
Waterhouse, W. L., and Watson, I. A. 1944. *J. Proc. Roy. Soc. N. S. Wales.* **77**, 138–144.

Present Status of Flax Diseases Other than Rust

Allison, C. C., and Christensen, J. J. 1938. *Phytopathology* **28**, 1.
Barker, H. D. 1923. *Minnesota Agr. Expt. Sta. Tech. Bull.* **50.**
Borlaug, N. W. 1945. *Minnesota Agr. Expt. Sta. Tech. Bull.* **168.**
Burnham, C. R. 1932. *J. Am. Soc. Agron.* **24**, 734–748.
Colhoun, J. 1948. *Ann. Applied Biol.* **35**, 582–597.
Culbertson, J. O. *et al.* 1952. *U. S. Dept. Agr. Farmers' Bull.* **2036.**
Flor, H. H. 1940. *Phytopathology* **30**, 749–760.
Forsyth, D. D., and Vogel, O. A. 1945. *J. Am. Soc. Agron.* **37**, 387–393.
Grossman, Helene. 1934. *Phytopathology* **7**, 545–583.
Houston, B. R., and Knowles, P. F. 1953. *Phytopathology* **43**, 491–495.
Kikuchi, M. 1940. *J. Fac. Agr. Hokkaido Imp. Univ.* **44**, 77–183.
Knowles, P. F., and Houston, B. R. 1953. *J. Am. Soc. Agron.* **45**, 408–413.
Kommedahl, T., and Christensen, J. J. 1950. *Phytopathology* **40**, 15.
Kommedahl, T., and Christensen, J. J. 1947. *Phytopathology* **37**, 13.
Kommedahl, T., Christensen, J. J., and Schwinghamer, E. 1950. *Phytopathology* **40**, 15–16.
Machacek, J. E., and Brown, A. M. 1945. *Sci. Agr.* **25**, 601–625.
Machacek, J. E., and Greaney, F. J. 1948. *Phytopathology* **38**, 803–807.
McKay, R. 1947. "Flax Diseases." Flax Development Board, Dublin.
Millikan, C. R. 1945. *J. Dept. Agr. Victoria* **43**, 305–313.
Millikan, C. R. 1951, *Dept. Agr. Victoria Tech. Bull.* **9.**
Moore, M. B., and Christensen, J. J. 1943. *Phytopathology* **33**, 1117.
Moore, M. B., and Christensen, J. J. 1946. *Farm & Home Sci.* (*Minnesota Agr. Expt. Sta.*) **3**, 7, 15.
Ray, C., Jr. 1945. *Phytopathology* **35**, 688–694.
Rodenhiser, H. A. 1930. *Phytopathology* **20**, 931–942.
Sackston, W. E. 1950. Ph. D. Thesis, University of Minnesota, St. Paul.
Schuster, Max. 1944. *Phytopathology* **34**, 356.
Schuster, M. L., and Anderson, E. J. 1947. *Phytopathology* **37**, 466–473.
Schwinghamer, E. A. 1952. *Phytopathology* **42**, 18–19.
Tervet, I. W. 1937. *Phytopathology* **27**, 531–546.
Tisdale, W. H. 1917. *J. Agr. Research* **11**, 573–606.
Tochinai, Y. 1925. *J. Coll. Agr. Hokkaido Imp. Univ.* **14**, 171–236.
Tsiang, Chen-Tong, 1947. Ph. D. Thesis, University of Minnesota, St. Paul.
Vanterpool, T. C. 1944. *Sci. Agr.* **24**, 268–270.
Wilson, Irene M. 1946. *Trans. Brit. Mycol. Soc.* **29**, 221–231.

Weeds

Blackman, G. E. 1952. *Jour. Exptl. Botany* **3**, 1–27.

Blackman, G. E., Holly, K., and Cox, E. G. 1952. *J. Agr. Sci.* **41**, 322–337.

Bothun, R. E. 1953. "A Preliminary Study of the Inheritance of the Reaction of Three Flax Crosses to 2,4-Dichlorophenoxyacetic Acid." *M. Sc. Thesis*, University of Minnesota, St. Paul.

Burrows, V. D., and Olson, P. J. 1952. *Ninth Annual Research Report.* North Central Weed Control Conference.

Chubb, W. O., and Mac Key, E. M. 1949. *Sixth Annual Research Report.* North Central Weed Control Conference.

Dunham, R. S. 1952a. *Down To Earth* **7** (4).

Dunham, R. S. 1952b. *Proc. North Central Weed Control Conf.*, p. 4.

Dunham, R. S., Larson, A. H., Heggeness, H. G., and Anderson, L. E. 1952. *Ninth Annual Research Report.* North Central Weed Control Conference.

Foster, J. R. 1949. *Sixth Annual Research Report.* North Central Weed Control Conference.

Friesen, H. A. 1949. *Sixth Annual Research Report.* North Central Weed Control Conference.

Friesen, George, and Olson, P. J. 1951. *Eighth Annual Research Report.* North Central Weed Control Conference.

Heggeness, H. G., and Le Tourneau, D. 1949. *Sixth Annual Research Report.* North Central Weed Control Conference.

Johnson, Virgil, and Robinson, R. G. 1952. *Minnesota Farm & Home Sci.* **IX** (3), 14.

Klosterman, H. J., and Clagett, C. O. 1949. *North Dakota Agr. Expt. Sta. Bi-Monthly Bul.* **XI** (3), 96–98

Leggett, H. W. 1950. *Seventh Annual Research Report.* North Central Weed Control Conference.

Mullison, W. R. 1951. *Plant Physiol.* **26**, 773–777.

Paatela, Juhani. 1949. *Valtion Maatalouskoetoiminnan Julkaisuja* **131**.

Paatela, Juhani, and Dunham, R. S. 1949. *J. Sci. Agr. Soc. Finland* **21** (4).

Robinson, R. G. 1949. *Agron. J.* **41**, 513–518.

Sexsmith, J. J. 1950. *Seventh Annual Research Report.* North Central Weed Control Conference.

Sharma, J. H. 1950. Ph. D. Thesis, University of Minnesota, St. Paul.

Shulstad, O. H. 1950. M. Sc. Thesis, University of Minnesota, St. Paul.

Swift, J. E. 1949. *Calif. Agr.* **3** (1), 11–14

Tandon, R. K. 1949. *Agronomy J.* **41**, 213–218.

Templeman, W. G., and Halliday, D. J. 1950. *Empire J. Exptl. Agr.* **18**, 169–76.

Wiese, A. F. 1953. Ph. D. Thesis, University of Minnesota, St. Paul.

Breeding

Bothun, R. E. 1953. "A Preliminary Study of the Inheritance of the Reaction of Three Flax Crosses to 2,4-Dichlorophenoxyacetic Acid." M. Sc. Thesis, University of Minnesota, St. Paul.

Carnahan, H. L. 1947. "Combining Ability in Flax, Linum usitatissimum." M. Sc. Thesis, University of Minnesota, St. Paul.

Carnahan, H. L. 1949. The Inheritance of Oil Content and Other Characters in Flax, and the Associations between characters in the cross of Dakota × Minerva. Ph. D. Thesis, University of Minnesota, St. Paul.

Chu, K. H. 1949. A Study of the Inheritance of Seed Size and Other Characters in a Cross between an Indian and a North American Variety of Flax. M. Sc. Thesis, University of Minnesota, St. Paul.

Chu, K. H., and Culbertson, J. O. 1952. "Studies of Inheritance of Seed Size and Other Characters in a Cross between an Indian and a North American Variety of Flax. *Agron. J.* **44,** 26–30.

Culbertson, J. O. 1949. "Objectives and Progress in Flax Breeding in the United States." Proc. Sixteenth Annual Meeting of the National Barley and Oil Seeds Committee, Barley Improvement Institute, Winnipeg, Canada.

Culbertson, J. O. 1952. "Registration of Improved Varieties of Flax V." *Agron. J.* **44** (No. 3), 153–154.

Culbertson, J. O. 1953. "Registration of Flax Varieties VI." *Agron. J.* **45,** 317–318.

Dillman, A. C. 1936. "Improvement in Flax." U. S. Dept. Agr. Yearbook, pp. 745–784.

Dillman, A. C. 1953. "Classification of Flax Varieties, 1946." *U. S. Dept. Agr. Tech. Bull.* **1064,** 56 pp.

Hayes, H. K., and Immer, F. R. 1942. "Methods of Plant Breeding." McGraw-Hill Book Company, New York.

Moseman, H. A. 1944. "Correlated Inheritance of Height, Seed Size, Seed Yields, and Other Characters in Flax." Ph. D. Thesis, University of Minnesota, St. Paul.

Myers, W. M. 1936. A Correlated Study of the Inheritance of Seed Size and Botanical Characters in the Flax Cross, Redwing × Ottawa 770B. *J. Am. Soc. Agron.* **28,** 623–635.

Ray, C., Jr. 1944. "Cytological Studies on the Flax Genus, Linum." *Am. J. Botany,* **31,** 241–249.

Technological Aspects of Trace Element Usage

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I. INTRODUCTION

The essentiality of certain trace elements for optimum growth and yield of plants is now fully recognized. The requirement for most of these elements was first established in painstaking physiological experiments, but sooner or later in many parts of the world soils were found so low in one or more of these essential elements that normal plant growth could not be obtained on them. Frequently the deficiencies resulted in abnormal growth and the development of symptoms previously believed to be due to invasion by pathogenic organisms. These deficiency symptoms, when recognized and identified, have indeed become valuable diagnostic aids. Trace element deficiency symptoms in important crop plants have recently been described and pictured in *Hunger Signs in Crops* (American Society of Agronomy and National Fertilizer Association, 1949) and by Wallace (1952).

Extensive analytical data on the content of trace or minor elements in crops have been collected (*e.g.*, Beeson, 1941; Bear *et al.*, 1948), though it has been found that, as with some of the major nutrient elements, the quantity present in a plant is not necessarily indicative of its requirement for that element but may far exceed it. The information as to the precise role of the trace elements in the nutrition of plants is less satisfactory, though their indispensability in certain enzyme systems is established (Wood, 1953). Furthermore, the transformations which some minor elements undergo in the soil and the activities of soil microorganisms in affecting their availability have been recognized (Waksman, 1952).

In agronomic practice in the United States the addition of trace elements has been found to be necessary for maximum yields on a diversity of soils and for various crops. The deficiencies which are overcome may arise for one of a number of reasons.

1. Acid, sandy soils, either because of the nature of the parent minerals, or through leaching, may be almost devoid of both major and minor elements.
2. Highly organic soils may not contain sufficient quantities of certain trace elements to support the crop plants now grown on them.
3. In calcareous, alkaline, or overlimed soils the trace elements, native or applied, may become converted to forms unavailable to plants.
4. Intensive cropping and use of commercial fertilizers not containing trace elements may result in the depletion of the original supply.

The fertilizer industry has been called upon to provide forms of trace element salts suited for meeting deficiencies. The present trend is toward the use of trace element salts in admixture with the various major fertilizer grades, with special mixtures being designed to meet

TABLE I

Estimated Consumption of Trace Elements in the United States in 1950, 1951, 1952 (in Tons)*

Element	1950	1951	1952
Boron, on basis of boron	1210 4	1372.4	1543.8
Copper, on basis of copper oxide (CuO)	5945.3	5524.8	5600.8
Manganese, on basis of manganese oxide (MnO)	5965.2	6275.9	4712.5
Zinc, on basis of zinc oxide (ZnO)	2008.9	2246.3	2499.4

* Lowe, James N. 1953. *National Fertilizer Rev.* 28, October-November-December, 8–9.

particular soil and crop requirements. Individual trace element salts and mixtures thereof are also made available for separate application to the soil, and, in addition, some neutral trace element salts, either alone or in association with insecticidal or fungicidal materials, are supplied for direct application to the foliage. The estimated consumption of trace element salts for fertilizer use in the United States is now substantial, as may be seen from the data for the years 1950 to 1952 (Table I).

II. SOURCES AND CHEMICAL PROPERTIES OF TRACE ELEMENTS

1. Sources

A large variety of ores are being utilized for production of trace elements. Most of these ores are found in the United States. Among these, the sulfides, oxides, carbonates, and silicates are largely used (Table II). The metallurgical industry has developed special processes to re-

TABLE II

Composition of Trace Element Ore Deposits in the United States

Metal	Sulfide	Oxide	Carbonate	Silicate
Copper	*Chalcocite:* Cu_2S 79.8% Cu	*Cuprite:* red Cu_2O—88.8% Cu	*Azurite:* $2CuCO_3 \cdot Cu(OH)_2$ 55.1% Cu	
Zinc	*Sphalerite:* ZnS 67% Zn	*Zincite:* ZnO 80.3% Zn	*Smithsonite:* $ZnCO_3$—52.1% Zn	*Willemite:* Zn_2SiO_4 58.6% Zn
Manganese		*Pyrolusite:* MnO_2 63.2% Mn	*Rhodochrosite:* $MnCO_3$—47.8% Mn	*Rhodonite:* $MnSiO_3$—41.5% Mn
Iron	*Pyrite:* FeS_2 46.7% Fe	*Magnetite:* Fe_3O_4 72.4% Fe	*Siderite:* $FeCO_3$ 62.1% FeO	
Boron		*Tincal:* $Na_2B_4O_7 \cdot 10H_2O$—36.5% B_2O_3		
Molybdenum	*Molybdenite:* MoS_2—60% Mo	*Wulfenite:* $PbMoO_4$ 39.3% MoO_3		
Cobalt	*Cobaltite:* CoAsS 35% Co *Linnaeite:* Co_3S_4 (+ iron & nickel)			

move impurities from the ores, since certain impurities, such as arsenic, selenium, and tellurium are highly toxic to both plant and animal life.

Through leaching with acids, the metals are converted into soluble salts (usually sulfates) and into slightly soluble basic salts. A list of the trace element salts most commonly used in agriculture is shown in Table III.

TABLE III

Trace Element Salts Most Commonly Used in Agriculture

I. Copper:	
Copper sulfate monohydrate—$CuSO_4 \cdot H_2O$	35% Cu
Copper sulfate pentahydrate—$CuSO_4 \cdot 5H_2O$	25% Cu
Basic copper sulfates—$CuSO_4 \cdot 3Cu(OH)_2$ (general formula)	
	(*a*) 13% Cu
	(*b*) 26% Cu
	(*c*) 34% Cu
	(*d*) 53% Cu
Basic copper carbonates:	
(*a*) malachite $CuCO_3 \cdot Cu(OH)_2$	57%
(*b*) azurite $2CuCO_3 \cdot Cu(OH)_2$	55%
II. Zinc:	
Zinc sulfate monohydrate—$ZnSO_4 \cdot H_2O$	35% Zn
Zinc sulfate heptahydrate—$ZnSO_4 \cdot 7H_2O$	23% Zn
Basic zinc sulfates—$ZnSO_4 \cdot 4Zn(OH)_2$	55% Zn
III. Manganese:	
Manganese sulfate (65%) $MnSO_4$	23% sol. Mn
Basic manganese sulfate $2MnSO_4 \cdot MnO \cdot 3H_2O$	40–49% Mn
IV. Borax:	
Fertilizer grade borate—$Na_2B_4O_7 \cdot 10H_2O$	34–44% B_2O_3
V. Iron:	
Ferrous sulfate—$FeSO_4 \cdot 7H_2O$	20% sol. Fe
Ferric sulfate—$Fe_2(SO_4)_3 \cdot 4H_2O$	17% sol. Fe
VI. Molybdenum:	
Sodium molybdate—$Na_2MoO_4 \cdot 2H_2O$	37–39% Mo
VII. Cobalt:	
Cobaltous sulfate—$CoSO_4 \cdot 4H_2O$	21–24% Co

2. *Physical-Chemical Properties*

In reviewing the physical-chemical properties of trace elements, it is interesting to note that the elements manganese, iron, copper, and zinc, which are extensively used for nutritional purposes, occupy adjacent positions in the periodic table. Thus it may be expected that certain similarities exist between these elements. This has been found to be true in many instances. For example, manganese, iron, and copper exhibit a resemblance in their oxidation-reduction potentials. Both manganese and iron may be readily oxidized from the di-valent to the tri-valent state; however, the manganous ion has greater chemical stability than the ferrous ion.

The equilibrium between di-, tri-, and tetra-valent manganese compounds, presented by Quastel (1946) in Fig. 1, is of special significance. This graph indicates that the oxidation-reduction reactions taking place in plant metabolism are apparently related to valence changes of the trace elements, in this case, manganese. T. Wallace (1952) has shown that through oxidation-reduction processes involving manganese and iron the required amount of oxygen may be furnished for plant respiration.

Copper may be readily oxidized from the monovalent to the divalent state. In agriculture, copper is commonly used in the divalent cupric state, which is very stable. A further similarity exists between copper and zinc in that each of these elements forms complex ammonium ions which seem to have a particular value in producing a more rapid recovery of plants from chlorotic conditions. Zinc maintains its chemical stability in the divalent form; it also exhibits amphoteric properties.

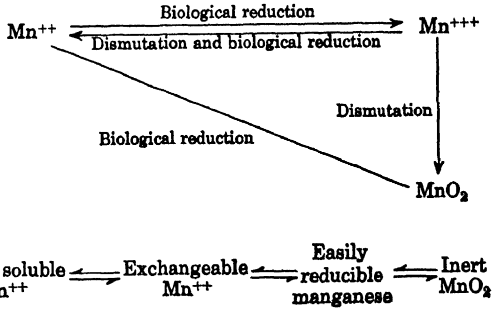

FIG. 1. Equilibrium between divalent, trivalent, and tetravalent forms of manganese compounds in which microorganisms play an important part.

Boron is in an adjacent position to carbon in the periodic table. In reference to this position, it may be stated that organic hydroxyacids, such as mannitol monoborate, containing both boron and carbon, play an important role in overcoming excessive alkalinity in plants.

III. CLASSIFICATION OF TRACE ELEMENT SALTS IN RELATION TO THEIR APPLICATION

Trace element salts employed in agriculture vary in composition and in physical-chemical properties. Their differences in solubility are being utilized in relation to the various methods of application. In Table IV the salts are classified according to their solubilities.

TABLE IV

Classification of Trace Element Salts According to Water Solubility

	Solubility in 100 parts	
I. Soluble Salts	Room temp.	100° C.
1. Copper sulfate	21.97	206
2. Zinc sulfate	41.9	80.8
3. Manganese sulfate	85 3	107
4. Borax	2.1	129
5. Ferrous sulfate	28.6	93.2
6. Sodium molybdate	76.2	98 3
II. Slightly Soluble Salts		
1. Basic copper sulfate	Trace	
2. Basic copper carbonate	Trace	
3. Basic zinc sulfate	Trace	
4. Basic manganese sulfate	Trace	

1. Readily Soluble Salts for Soil Treatment

The soluble trace element salts are most frequently applied in the form of sulfates. These salts have a rather strong acid reaction and are used extensively for soil treatment, alone and in combination with major fertilizers (N-P-K). This method has long been recognized as the most economical means of applying trace elements.

2. Slightly Soluble Salts for Foliar and Branch Treatment or Trunk Injection

a. Foliar and Branch Treatment. For the most effective foliar treatments, it is necessary that the chemical and physical properties of trace element salts be such that no injury to the foliage may occur. This is especially true since leaf cells are sensitive to both acid and highly alkaline materials. It is a primary requirement that the material used for foliar treatment be chemically neutral and only very slightly soluble in water. These neutral salts, usually in the form of basic sulfates, are entirely safe for direct foliage treatment, even on sensitive crops.

For the most effective foliar correction of nutritional deficiencies in plants, it is necessary to secure complete coverage of the foliage. This helps to furnish the maximum amount of nutrients for assimilation through the foliar area. For most plants, this area is many times greater than that of the soil in which the plants are growing. To secure thorough coverage of such a vast area of leaves, the materials must be in a finely divided state. The fineness of the particles also helps to secure better adherence.

Recent developments in the manufacture of neutral trace element salts have made it possible to secure this extreme subdivision of material. The fine particle size of these salts renders them suitable for use in the form of either spray or dust. Field tests by Isaacs and Hester (1953) and by Tukey *et al.* (1952) show that the neutral trace element salts are compatible with most of the commonly used insecticides and fungicides. As a result of this compatibility, both nutritional and pesticidal materials may be safely used in a single application. This is recognized as the most economical method of foliar treatment.

It has been found beneficial to employ foliar treatment when it is necessary to avoid interference from the soil and other elements. This is especially true in the case of crops on highly alkaline soils, which tie up the trace elements, and on highly acid soils, which are subject to leaching.

Direct foliage treatment is of special value in cases where the deficiency has become so acute as to be conspicuous on the foliage. The most rapid response to foliar applications of the nutrient elements is observed when the materials are applied early in the season.

Foliar treatments are now employed on a commercial scale in Florida, on sweet corn, beans, tomatoes, celery, and citrus. Several other states are using foliar treatments for sweet corn, small grains, pasture, beans, and cauliflower.

In many cases, it is expedient to supplement soil applications of trace elements with foliar treatment. This practice is highly beneficial, since the additional quantities help to satisfy the greater demand for trace elements by plants during stages of maximum growth.

b. Injection. The neutral trace element salts are also used for injection into ornamental tree trunks. In practicing this method of application, two procedures may be followed: (1) the dry salts are placed in holes bored into the sapwood of the tree; and (2) water suspensions of the salts are forced into holes in the sapwood with a syringe.

3. *Insoluble Salts for Soil Treatment*

A new type of trace element carrier under current investigation is the insoluble silicates. These are high-temperature–fused materials, glasses, in which are incorporated the trace elements. These salts possess extremely low solubility and release trace elements for plant assimilation at a very slow rate when applied to the soil.

IV. MIXING TRACE ELEMENTS WITH MAJOR FERTILIZERS

The question frequently arises as to whether the major fertilizer materials available on the market have sufficient amounts of trace elements for common crops. Millar and Gillam (1940) conducted investigations to determine the trace element contents of representative commercial fertilizers. The results of their analyses show that, in most cases, these fertilizers contained insufficient quantities of trace elements to meet the requirement of deficient crops. In view of this, the fertilizer industry is now beginning to add required quantities of trace element salts to a number of their fertilizer mixtures. Recent surveys show that many growers prefer to apply trace elements in the form of mixtures with major fertilizers.

1. Advantages of Using Trace Elements in Combination with Major Fertilizers

1. The primary advantage is that the grower is able to apply both trace elements and major fertilizers in a single operation. This eliminates the expense of separate handling and application.
2. The most efficient use of fertilizer materials for plant growth can be realized when both major and trace elements are furnished.
3. More uniform distribution of trace elements is secured when they are applied in the form of mixtures.
4. The physical properties, such as free flow and noncaking, are not affected by incorporating the trace elements into major fertilizers.
5. Tests relating to moisture content show that there is no increase in moisture absorption when trace elements are used in combination with major fertilizers.

2. Methods of Introducing Trace Elements into Major Fertilizers

a. Before Ammoniation. Trace elements may be successfully added to major fertilizers before the ammoniation process, provided some preliminary mixing is employed. In this case, the acid character of superphosphate provides protection against interaction between trace elements and ammonia.

b. While Bringing to Grade. Trace elements may be readily incorporated into major fertilizers during the process of bringing the mixture to grade after ammoniation. In this operation, it is essential to avoid segregation of the major fertilizers which may occur as a result of (1) exceedingly low moisture content (overdrying), (2) wide variation in particle size, and (3) great difference in the N-P-K ratio.

c. In Blunger Prior to Granulation. In preparing granulated fertilizers, trace elements may be added in the blunging, or blending, operation just prior to granulation. The addition of trace elements, in this case, in no way affects the physical properties of the resultant product.

3. Quantities of Trace Elements Added to Major Fertilizers

The quantities of trace elements added to major fertilizers will vary according to the crop and the character and composition of the soil being treated. For example, 50 to 75 pounds of copper sulfate per acre are required for the muck soils of Florida, Michigan, and New York. The manganese requirement of these soils is also high. Large quantities of boron are used with regular fertilizer materials for pasture crops, especially alfalfa. However, for average soils, certain standard mixtures of trace elements and major fertilizers are being used on a commercial scale.

4. Physical Conditions of Major Fertilizers Required for Mixing with Trace Elements

The most desirable physical conditions of the final mixtures of major fertilizers containing trace elements can be secured through the following:

1. Proper curing of the N-P-K materials to complete the chemical reaction between the major elements.
2. Control of the moisture content of the major fertilizer.
3. Avoiding an excessive concentration of limestone and thus eliminating a high alkalinity in the mixture.
4. Protection against extreme accumulation of moisture during storage.

In mixing major fertilizer materials (N-P-K), it is common practice to add some inert ingredients as a makeweight to balance the formula to a specified grade. The order of adding trace elements with respect to the inert ingredient must be carefully determined for the purpose of securing their uniform distribution throughout the mixture. When it is necessary to add highly alkaline materials, such as limestone or dolomite, it is essential that the trace elements be added after the alkalies have been thoroughly mixed with the major fertilizers. This allows for the alkaline materials to react with superphosphate and thus to minimize interaction with the trace elements.

It is important to guard against the addition of any ingredient which might cause caking or segregation of the major fertilizers. In fact, certain conditioning agents are often added to prevent caking and thus to aid in securing a more uniform distribution of trace elements throughout the mixture. Vermiculite and sulfonated wetting agents have been found to be especially suitable.

5. *Solubility of Trace Elements in Combination with Major Fertilizers*

Comparative results on the solubility in water, ammonium acetate, or ammonium citrate of the trace element salts mixed with major fertilizers are presented in Table V. The solubilities of copper and zinc salts added after ammoniation of N-P-K fertilizer are slightly higher than the solubilities of these salts added before ammoniation. These results indicate it is more advantageous to add trace element salts to N-P-K materials after the ammoniation process is completed.

TABLE V

Solubilities of Trace Element Salts Mixed with Fertilizer by Various Methods*

	Trace element salts added before ammoniation		Trace element salts added after ammoniation		
	Mixture analyzed immediately				
Solvent	Copper, %	Zinc, %	Manganese, %	Copper, %	Zinc, %
Water	77.78	73.40	51.82	88.97	74.50
Ammonium acetate	91.27	78.09	74.75	73.31	89.95
Ammonium citrate	92.07	91.97	97.58	94.12	92.69
	Mixture analyzed after aging 2 weeks				
	Copper, %	Zinc, %	Manganese, %	Copper, %	Zinc, %
Water	18.45	21.65	50.85	24.07	28.10
Ammonium acetate	40.99	42 20	45 01	84 55	79.60
Ammonium citrate	83 27	85 47	91.45	95 93	87 94

* A. A. Nikitin and Josephine W. Rainey, *Agron. J.* 44, 1952, pp. 541–546.

It is necessary to differentiate between acid-forming and non-acid-forming fertilizers. The character of reaction of the fertilizer mixture may affect the solubility of trace element salts as a result of the varying phosphate content of the mixture and of the type and quantity of alkali added. Some decrease in solubility of the manganese salt is noted when it is mixed with non-acid-forming fertilizers adjusted with lime. There is considerably less change in the solubilities of copper and zinc salts, as shown in Fig. 2.

There is some variation in the performance of calcium lime and magnesium lime, owing to two factors:

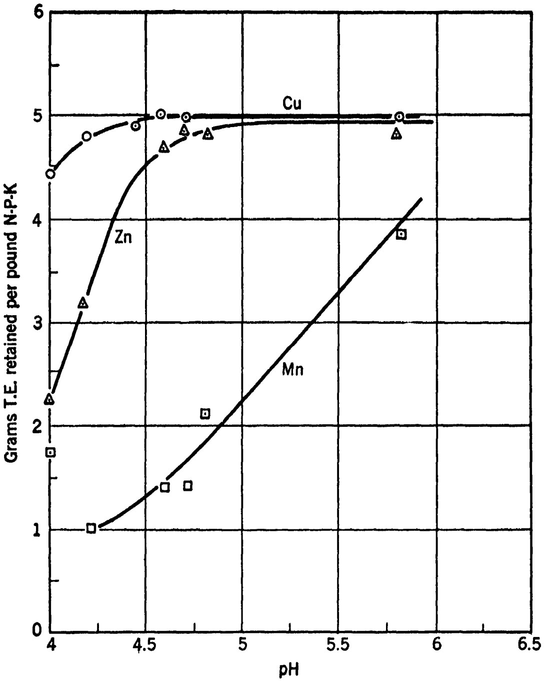

FIG. 2. Solubility of Cu, Zn, and Mn in combination with N-P-K adjusted with lime to various hydrogen ion concentrations.

1. Difference in solubility of the sulfates.
2. Difference in amount of water of crystallization.

V. FACTORS RELATING TO AVAILABILITY OF TRACE ELEMENTS

1. Relationships between the Elements

Synergisms and antagonisms between the nutrient elements have been found by several investigators to affect the availability of the elements. Martin *et al.* (1953) have found that an excess of potassium or sodium exerts a powerful antagonistic action in reducing manganese assimilation by citrus seedlings. The presence of 15 per cent potassium reduced manganese to the deficiency level. Martin's results prove that the total amount of soil manganese cannot be considered as a criterion of its toxicity or reliably indicate whether the supply of manganese to the plant may be adequate or insufficient.

Hill *et al.* (1953) observed that there is a "consistent antagonism between cobalt and manganese." In this case, manganese tends to reduce the toxic effect of higher concentrations of cobalt, and cobalt lessens the severity of manganese toxicity. Hill and co-workers found high concentrations of iron in the soil to be antagonistic in relation to the assimilation of cobalt. Nicholas and Thomas (1953) have noted the antagonistic action between iron and cobalt in the presence of a high cobalt content.

Results secured by Somers and Shive (1950) show that it is necessary to maintain a certain ratio between iron and manganese in order to avoid excessive accumulation of manganese and to render iron more readily available. For most crops, the iron-manganese ratio should be about 2/1. Mazé (1936) found that a few crops, such as maize, require that the ratio be 7/1.

Information secured by Collander (1941) shows that the absorption of some cations can be depressed by other cations exerting antagonistic action. Thus the use of high concentration of potassium for correction of its deficiency may create or accentuate a magnesium deficiency, resulting in a poor yield. However, magnesium does not interfere with potassium absorption.

The antagonistic action between the elements is employed in many cases to overcome the toxic effects of certain elements. For example, in the Everglades region of Florida the molybdenum content of the soil is high enough to be toxic to animals grazing on the pastures. Copper sulfate is being used to overcome molybdenum toxicity and at the same time to correct copper deficiency.

The antagonism of lime for boron is being effectively utilized to permit the use of boron with a fair degree of safety. It can safely be used at higher concentration on some crops, such as alfalfa, beets, and crucifers. In contrast, small grains and beans can tolerate only very low concentrations of boron. For emergency cases, lime is being effectively employed to reduce the toxic effect of boron.

2. *Soil Conditions*

Soil conditions are fundamentally responsible for the quantity of trace elements which can be assimilated by plants. The composition of the soil must be carefully examined to determine the rate at which trace elements can be efficiently employed. From studies on the safe application of trace elements to different types of soils, Blair and Prince (1936) show that small quantities of trace elements will produce quick response on most acid, sandy soils. In contrast, marl soils, which greatly interfere with the assimilation of nutrient elements, permit their use at higher concentrations. These facts illustrate that soil conditions determine the quantity of trace elements which can be applied beneficially. In cases where the soil ties up the trace elements to such an extent as to cause deficiency, more than one application may be necessary.

The organic matter present in the soil often causes a deficiency of the nutrient elements. This is especially significant with regard to copper and zinc. According to Sommer (1945), large amounts of copper are required to correct its deficiency in soils high in humus. The results of Jones *et al.* (1936) and Camp (1945) show that even in acid soils containing large amounts of organic matter, zinc deficiency commonly occurs as a consequence of its interaction with the organic matter.

It has been found that the stage of growth at which trace element applications are made is significant with respect to concentration. For most plants, foliar applications of trace elements are highly beneficial when made early in the season. Rademacher (1939) found that for oats the copper requirement is highest in the early stages of growth prior to flowering. A late treatment with copper does not aid in producing normal seed development. Wallace (1950) and Erkama (1950) have pointed out that correction of trace element deficiencies in peas is most effectively achieved by spraying the peas at blossoming time.

Steenbjerg (1950) has observed that manganese is available in the soil at higher concentrations in spring and summer than in fall and winter. Thus, for fall and winter crops, manganese can be applied at higher concentrations than for spring and summer crops.

Forsee (1952) has found that twenty-five pounds per acre of copper sulfate disked into peat soils, six weeks before planting, will produce maximum copper response, provided moisture conditions are satisfactory. If, however, the copper sulfate is applied just before planting, a considerably larger quantity is required.

VI. SUMMARY

The metallurgical industry has been able to recover trace element metals from the ores and to convert them into salts suitable for agricultural purposes. It was necessary to develop special processes for the removal of such toxic elements as arsenic, selenium, and tellurium. As a result of large-scale production of trace element salts, their use has become very economical.

In using trace element salts for correcting deficiencies it was found that the acid radicals should also be taken into consideration. Neutral salts, usually basic sulfates, have been found highly suitable for direct foliage treatment, since they are compatible with most insecticidal and fungicidal materials. The soluble sulfate salts have been found particularly valuable for soil treatment, since sulfur is also an essential element for crops. A standard formula for trace element mixtures with major fertilizers has been developed with the idea of furnishing nutrient elements in a balanced ratio.

Proper curing of major fertilizer materials and the correct order of adding trace elements with N-P-K are necessary precautions in mixing these materials in order to protect trace elements against the effects of high alkalinity. Certain conditioning agents are being used to avoid caking and segregation of the fertilizer materials.

Antagonistic action between the nutrient elements may affect the rates of assimilation and thus induce deficiencies. By determining the relationships between the nutrient elements, interference can be greatly minimized. Antagonistic actions have made it possible to overcome toxic effects of such elements as molybdenum. Excessive amounts of N-P-K can also induce deficiencies of the trace elements if the latter are present in borderline quantities.

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REFERENCES

American Society of Agronomy and National Fertilizer Association. 1949. "Hunger Signs in Crops" (rev. ed.).

Bear, F. E., Toth, S. J., and Prince, A. L. 1948. *Soil Sci. Soc. Amer. Proc.* **13,** 380–384.

Beeson, K. C. 1941. *U. S. Dept. Agr. Misc. Publ.* **369.**

Blair, A. W., and Prince, A. L. 1936. *Soil Sci.* **42,** 327–333.

Camp, A. F. 1945. *Soil Sci.* **60,** 157–164.

Collander, R. 1941. *Plant Physiol.* **16,** 691–720.

Erkama, J. 1950. "Trace Elements in Plant Physiology," p. 97. Chronica Botanica Company, Waltham, Massachusetts.

Forsee, W. T., Jr. 1952. *Proceedings of the Florida State Horticultural Society,* pp. 154–159.

Hill, A. C., Toth, S. J., and Bear, F. E. 1953. *Soil Sci.* **76,** 273–284.

Isaacs, R. L., Jr., and Hester, J. B. 1953. *Agr. and Food Chem.* **1,** 239–240.

Jones, H. W., Gall, O. E., and Barnette, R. M. 1936. *Florida Agr. Expt. Sta. Tech. Bull.* **298.**

Lowe, James N. 1953. *Natl. Fertilizer Rev.*, **28,** October–November–December, 8–9.

Martin, J. P., Harding, R. B., and Murphy, W. S. 1953. *Soil Sci.* **76,** 285–295.

Mazé, P. 1936. *Ann. Rev. Biochem.* **5,** 525–538.

Millar, C. E., and Gillam, W. S. 1940. *J. Am. Soc. Agron.* **32,** 722–725.

Nicholas, D. J. D., and Thomas, W. D. E. 1953. *Plant and Soil* **5,** 67–80.

Nikitin, A. A., and Rainey, Josephine W. 1952. *Agron. J.* **44,** 541–546.

Quastel, J. H. 1946. *Proc. Roy. Inst. Gt. Brit.*, 22 pp.

Rademacher, B. 1939. *Bodenkunde u. Pflanzenerähr.* **64,** 80–108.

Somers, I. I. and Shive, J. W. 1942. *Plant Physiol.* **17,** 582–602.

Sommer, A. L. 1945. *Soil Sci.* **60,** 71–79.

Steenbjerg, F. 1950. "Trace Elements in Plant Physiology," pp. 87–95. Chronica Botanica Company, Waltham, Massachusetts.

Tukey, H. B., Ticknor, R. L., Hinsvavr, O. N., and Wittwer, S. W. 1952. *Science,* **116,** 167, 168.

Waksman, Selman A. 1952. "Soil Microbiology," p. 242. John Wiley & Sons, New York.

Wallace, T. 1950. "Trace Elements in Plant Physiology," p. 96. Chronica Botanica Company, Waltham, Massachusetts.

Wallace, T. 1952. "The Diagnosis of Mineral Deficiencies in Plants," pp. 8–14. Chemical Publishing Co., New York.

Wood, J. G. 1953. *Ann. Rev. Plant Physiol.* **4,** 4–8.

Crop Adaptation and Climate

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I. INTRODUCTION

Crop adaptation refers in a broad sense to the relationships between the principal environmental factors and the growth response of crop plants. Largely ecological in character, this branch of plant science may be considered a synthesis of important elements of geography, physiology, genetics, meteorology, and agronomy. Because of its direct relationship to food production, the adaptation of crops is of vital concern to all.

Political and economic developments during recent years have brought forcibly to our attention the necessity of a world viewpoint on crop production. The long-term outlook for the world's food supply is a controversial question. It has been estimated by Huxley (1950) and others that during the next 50 years the population of the world may increase from 2.5 billion to 3 billion. An alarming view of this rapid increase in population and the possible failure of food production to meet essential requirements has been presented by Vogt (1948). Less pessimistic, although worthy of most serious consideration, are the studies of Stamp (1952) and Shaw (1953). The people of the United States will play an increasingly vital role in attempts to solve this food problem. At the outset, it seems obvious that crop production must be increased and made more efficient, if the demands for food are to be met. One of the most important aspects of this problem is the adaptation of the numerous crops and varieties grown. A more complete understanding of the specific environmental requirements of our present crop varieties and of the breeding material now being observed for possible use in future varieties has been emphasized by Whyte (1946).

The natural limits of crop adaptation are imposed by the important ecological factors. Primary among these factors is the climate. Crops such as rubber, cacao, and bananas are limited to frost-free belts, because of their rather exacting temperature requirements. Wheat, in contrast, is grown successfully over a wide range of climatic conditions, from the Equator to relatively high latitudes (55° to 60°) in Canada, Finland, and Siberia. The greater tolerance of wheat to this wide temperature range is due in part at least to the greater genetic diversity found among the world's wheats, as compared with that found in cacao or bananas.

The farmer is aware of crop adaptation in recognizing that some crops do well in his region whereas others do not. He knows that choice of varieties is especially important in full season crops like corn and soybeans. He is aware of annual differences in length of growing season and in frost hazards he may face. He has experienced drought and knows that by the use of certain varieties and management practices he may increase or decrease the chances of avoiding serious losses.

To the plant breeder, adaptation refers to something even more specific. He pictures any species or variety as a more or less infinite population of plants having a certain range of genetic diversity, depending largely on its origin and mode of reproduction. This diversity offers an opportunity for selection of biotypes that may be better adapted than presently grown strains, either for the area where the crop is now grown or for new areas. Better adaptation may refer to higher yield of forage or seed, capacity to cope with unfavorable soil conditions, ability to resist insect or disease attack, or more favorable chemical composition. The plant-environment relationships involved are many and exceedingly complex.

Billings (1952) has defined the environment of a plant as all of the external forces and substances affecting growth, structure, and reproduction. It is well known, but too often insufficiently emphasized, that the environment is dynamic, constantly changing from season to season, day to day, and hour to hour. To gain a better understanding of the relationships between the important environmental factors, such as climate, soil, and other organisms, and the growth and reproduction of the plant, requires that basic and complex principles of crop geography and ecology be investigated. High on the list of important relationships are those dealing with the climatic elements, precipitation, temperature, and light, as they relate to the adaptation of old varieties of crops and to the development of new ones. It is the purpose of this paper to review some of the many contributions to the development of principles on which these relationships are based.

II. ENVIRONMENT AND DISTRIBUTION OF PLANTS

1. Principles of Plant Geography

a. Climatic and Edaphic Factors. To provide an explanation of the distribution of plants throughout the world, six basic principles have been given by Good (1931, 1953). It would seem logical to apply these principles, insofar as is possible, to the adaptation and distribution of crop plants. They may be stated briefly as follows:

1. Plant distribution is primarily controlled by the distribution of climatic conditions.
2. Plant distribution is secondarily controlled by the distribution of edaphic factors.
3. Great movements of species and floras have taken place in the past and are apparently still continuing.
4. Plants movement (plant migration) is brought about by the transport of individual plants during their dispersal phases.
5. There has been great variation in climate, especially at higher latitudes, since angiosperms became prominent.
6. Some variation has occurred during the same period in the relative distribution and outline of land and sea.

Good (1953) states that the facts of plant geography everywhere show that plant distribution is basically dependent on climate. Edaphic factors are secondary, because they are often controlled by climatic factors. Further, Good states that although the climatic factors, temperature, moisture, light, and air movement, control the extent of distribution, soil factors may control its intensity. Thus, it might be said that climatic factors will determine whether corn shall be a potential occupant of a given area, whereas soil factors may determine largely whether corn actually will be grown and in what abundance.

b. The Evolutionary Factor. Probably even more fundamental, and underlying all the climatic and soil factors affecting plant distribution, is the factor of evolution itself. One of the striking facts of all biology is the amazing diversity found in organisms. This diversity is the product of evolution, and as Darwin recognized, is due to the response of living matter to the wide range of environments found on the earth. The periodic production of new forms is the essence of evolution. Temperature, moisture, and other conditions of the environment may be considered direct factors which determine where plants can grow, but as Good (1953) has aptly noted: "Evolution is the medium in which the picture of plant distribution is painted." This implies that plant geography is dynamic and that in the study of adaptation we are dealing with plants and conditions constantly undergoing change.

Movement or migration of plants is of great importance if a species is to occupy anything like its potential range. Although the ordinary plant is incapable of movement during its vegetative phases, because of the attachment of its roots to the soil, movement is accomplished during its seed or dispersal phase. Dispersal of seed or propagules may explain how migration takes place but does not explain why changes in the climate may result in such movement of plants.

c. The Theory of Tolerance. As a basis for an explanation of just how and why it is possible for plant distribution to result from movement and migration under climate change, a concept of specific tolerance was developed. This concept, proposed by Good (1931), amplified and extended by Mason (1936), Cain (1944), and Good (1953), is now considered one of the basic principles of modern plant geography. The Theory of Tolerance may be stated as follows:

> "Each and every plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions. This range represents the tolerance of the species to external conditions.
>
> "The tolerance of a species is a specific character subject to the laws and processes of organic evolution in the same way as its morphological characters, but the two are not necessarily linked.
>
> "Change in tolerance may or may not be accompanied by morphological change, and morphological change may or may not be accompanied by change in tolerance.
>
> "Morphologically similar species may show wide differences in tolerance, and species with similar tolerance may show very little morphological similarity.
>
> "The relative distribution of species with similar ranges of tolerance is finally determined by the result of competition between them.
>
> "The tolerance of any larger taxonomic unit is the sum of the tolerance of its constituent species."

Taylor (1934) and Mason (1936) suggested that the extremes of a climatic factor, temperature, for example, may be more important than the mean temperature in limiting the area occupied by a species. Also, they called attention to the existence of narrower ranges of tolerance during critical stages. Thus it is clear that the range of tolerance to temperature or any other external factor may not be the same at germination, emergence, anthesis, or seed maturation.

Three kinds of changes are implied in the tolerance theory as explained by Good (1953), including (1) rate of evolutionary change, (2) rate of environmental change, and (3) rate of movement of a species by means of dispersal. Under natural conditions it is assumed that evolutionary change is slower than the other two.

If the tolerance of any taxonomic unit is made up of the tolerances of its constituent parts, it logically follows that the tolerance of any population may be essentially like or unlike that of another population of the same species. The tolerance of corn, for example, is composed of many ranges of tolerance to individual factors of the environment, but probably one of these will become limiting. A narrow range of tolerance toward temperature will control distribution, even though tolerance toward rainfall and soil conditions may be much wider.

Differences among crop species, particularly in their modes of fertilization, would be highly important in determining tolerance ranges. In general, as suggested by Darwin (1872), widely ranging species vary most. Cross-fertilizing species, especially those belonging to genera widely distributed, would appear to offer greater opportunities for selection of varieties adapted to widely varying environmental conditions, than would self-fertilizing or endemic species.

d. The Holocoenotic Environment. Although it is possible to study the effects of individual factors, such as temperature or light, on plant growth in the laboratory or greenhouse, it probably is impossible to speak of such effects as typical of those produced in nature by the same specific factors. This is because the environmental complex must be considered as a whole, or, as stated by Allee and Park (1939) and emphasized by Klages (1942), Cain (1944), and Billings (1952), the environment is holocoenotic. This principle has been shown in some detail by Billings (1952) in diagrammatic representation. Fifteen factors, including temperature, water, soil, wind, parent material, solar radiation, other plants, animals, fire, and man, are shown in direct relationship to the plant and in interrelationships among one another. This plant-environment relationship is so complex that Cain (1944) has suggested that it may never be possible to subject it to a complete analysis, and, therefore, many ecological problems may be insoluble in the mathematical sense. In spite of these difficulties, Major (1951) has proposed a formula for quantitative studies of environmental interrelationships. In the laboratory and greenhouse, great strides have been made in determining with great accuracy the response of plants to climatic factors. Particularly fruitful in studying the effects of the diurnal range in temperature and of alternating temperatures, as well as some of the interacting light-temperature effects, has been the work of Went and his associates (1950). The principle of limiting factors, developed by Liebig (1862), Blackman (1905), and others, has been widely accepted. It was pointed out by Billings (1952) that though the thesis of this principle is that plant growth is limited when any factor of the environment falls below the minimum required for a particular species, growth may be limited also when a factor goes above the maximum tolerance by the plant for that factor.

The concept of limiting factors and that of the holocoenotic environment are not incompatible. Billings has given the example of an arid area brought under irrigation. Water deficiency was the limiting factor for plant growth. If water is added to the desert adjacent to the cultivated land, weeds soon replace the native desert shrubs and grasses. Soon, greater competition is offered to the crop plants in the cultivated portions. Although many factors interacted as a result of bringing it to the land, water itself was the limiting condition.

III. ADAPTATION

1. *What Is Meant by Adaptation*

An adaptation, according to Daubenmire (1947), is any feature of an organism that is of definite value to its existence under the conditions of its habitat. Such features may allow the plant to make fuller use of the nutrients, water, heat, or light available or may aid in protection against adverse factors. After accumulating adaptations for many, many generations, a great number of the characteristics of each species are adaptive. Plant may have physiologic adaptations resulting in resistance to insects or diseases. They may have morphologic adaptations such as height differences, ability to spread, and ability to resist lodging.

From the genetic viewpoint, Dobzhansky (1951) suggests that adaptive values, or Darwinian fitness, may be considered as a statistical concept describing the reproductive efficiency of a genotype in a certain environment. He states further that although the adaptive value of a homozygote for a lethal gene is zero, the vigor of the plant, its viability, is only one of the variables which determine adaptive value. The degree of perennialism, the frequency and duration of reproductive periods, the efficiency of pollination mechanisms, the number of viable seeds produced, and the competing ability of seedlings, all are important.

Adaptation under cultivation would seem to be similar to adaptation in nature and is of utmost importance to the plant breeder. Darwin (1872) undoubtedly arrived at many of his conclusions regarding fitness and survival value in general from his observations on variability and survival among domestic animals and plants.

a. Direct Adaptation. The concept of direct adaptation holds that the organism is altered or molded in direct response to a particular need. It implies also that adaptations are changes brought about during the life of the individual and that they are transmitted to subsequent generations. Daubenmire (1947) has emphasized that "purposive" adaptation beliefs probably explain the use of terms such as "food storage" when we mean "food accumulation," or our speaking of certain plants as "avoiding" acid soils.

It is well known that when genetically identical plants or clone members are grown in widely different habitats, the phenotypic appearance may be quite different. Such changes are known as modifications, or ontogenic variations, and are not transmitted through the germ plasm to the offspring. That some of these modifications are transmitted to succeeding generations is one of the basic concepts of Lamarckianism, and even today the idea has its followers. In order that the issue be not confused, it should be pointed out that some variations induced by the environment, such as increased cold resistance by hardening and increased drought tolerance by exposure to drought are temporary beneficial effects and might be considered temporary adaptations. In general, however, adaptations will refer to changes in genetic composition, rather than to temporary adjustments or modifications.

b. Indirect Adaptation. The genetic concept of adaptation is that adaptations arise by the selective action of the environment on the genetic variations available. The principle of natural selection was proposed by Darwin (1872). This implies that from a population of genetically mixed types, some are more likely to produce surviving progeny than others. Expressed in the light of the Theory of Tolerance, some genotypes have a greater range of tolerance than others, or perhaps their tolerance is in closer harmony with the specific environmental conditions. Dobzhansky (1951) has stated that in a mixture of genetically distinct types, certain genes, gene complexes, and chromosome structures will become more, and others less, frequent in succeeding generations through natural selection.

(*1*) *Sources of variability.* The source of variability is fundamentally mutation. As Dobzhansky (1950) has pointed out, the environment influences evolution at two levels, gene mutation and natural selection. If we think of mutation as a chemical change, such as a shift in position of a side chain of a complex molecule, or other change in configuration, it is logical to assume that it may have been brought about by a change in temperature, moisture, light, or combinations of several environmental factors. At the level of natural selection, it is easy to visualize that variations in temperature, moisture, and other factors may result in the survival of certain individuals and the loss of others. In addition to mutation, genetic variability is increased by recombination, duplication, loss or addition of genes, chromosome segments, whole chromosomes, or genomes.

(*2*) *Natural selection.* Natural selection has been a powerful force, both in the development of native vegetation and in the development of crop varieties. In domesticated plants, as shown by Mangelsdorf (1952), the factor of competition has either been largely removed or at least changed. Crop varieties which produce the highest yields under cultivation may not persist as well as lower yielding ones when grown in direct competition in mixtures. This has been demonstrated strikingly in small grains by Klages (1936), Harlan and Martini (1938), Laude and Swanson (1942), Suneson and Wiebe (1942), and others.

In contrast, however, many superior local strains of forage plants have been produced from highly heterozygous material, under severe competition, through years of natural selection. Such are a number of highly vigorous and well-adapted strains of red clover found in the eastern half of the United States. In many strain trials at the Iowa Agricultural Experiment Station during the past several years, no bred varieties have outyielded these local strains which were grown for many generations on one farm or in one locality.

Sylven (1937) has given a striking example of natural selection in white clover. A German variety increased in productivity as much as 37% when grown for three generations in Sweden. Other introduced strains, apparently not so variable in genetic make-up, showed a gain of from 0 to 15% during the same period.

Kemp (1937) noted in Maryland that natural selection in permanent pastures resulted in the ascendancy of those growth types of several species which are best adapted to survive grazing conditions.

Åkerberg (1948) found that local strains of red clover having dissimilar characteristics, such as yielding ability, earliness or lateness of maturity, and varying degrees of perennialism, were distributed from south to north in Sweden according to climatic conditions. In Norrland, most naturalized strains are earlier in maturity than those from central Sweden, an adaptation to the temperature- and light-climate of the high northern latitude. By repeated sowing for several generations, strains brought from Svalöv have yielded from 10% to 15% more than the same strains introduced directly from southern Sweden.

Donald (cited by Gregor, 1944) found natural selection rapid in Australia, based largely on moisture tolerance. Two varieties of sub-clover (*Trifolium subterraneum*), one early and one midseason in maturity, were planted together in a relatively dry area at the Adelaide Experiment Station. In a few generations the clover population was composed primarily of early genotypes. Moisture conditions were unfavorable when late genotypes came into bloom, so that early types predominated in the production of seed. In another part of the same experiment, the mixed seeding of sub-clover varieties in a relatively wet area at Adelaide Hills resulted in a population of predominantly midseason and late-maturing strains.

(3) *The ecotype concept.* It appears obvious that within a highly variable species different climatic races or forms may develop. These races of biotypes, distinguished by their specialized ecological preferences, are often called ecotypes. The ecotype concept has been ably presented by Turesson (1922a, 1922b, 1927, 1930), Stapledon (1928), Gregor (1931, 1944, 1946), Clausen *et al.* (1940, 1941, 1947), Clausen (1949, 1951), Turrill (1940, 1946) and others. An ecotype is defined as a group of biotypes especially adapted to a specific environmental niche. It follows that there may be climatic, edaphic, and biotic ecotypes. It has been suggested also that agricultural varieties might be considered as agro-ecotypes.

Turesson demonstrated that if several ecotypes from contrasting environments are grown together in one location, they and also their offspring exhibit distinctive genetic differences. These hereditary differences do not represent random variability, but rather the "genotypic response" to the various environments present in the locations where the ecotypes evolved. The experimental method for studying ecological races was advanced greatly by the reciprocal transplant scheme used so effectively by Clausen, Keck, and Hiesey. Clone members (rooted cuttings) from individual plants were compared in three contrasting environments at sea level, 5500-ft., and 12,000-ft. elevations. With genetic variation eliminated, effects of environment could be determined.

One of the most striking studies by these workers is that of the California races of *Potentilla glandulosa.* A coastal ecotype occurs at low elevations characterized by a dry summer and equable winter. Two races occur on dry slopes and in meadows of the Sierra Nevada foothills. Here the climate is hot in summer, with snow in winter and abundant rainfall in spring. Then there are the alpine and subalpine ecotypes which are found in the high Sierras, where the winters are long and cold, rainfall abundant, and the growing season short. The coastal and foothill ecotypes do not grow normally when transplanted to each other's environment, although they may survive for some time. The coastal race becomes dormant in winter in the foothills, whereas the foothill race tends to grow the year round in the coastal habitat. Neither of these ecotypes produces seed when grown under alpine conditions. The alpine races are dwarflike in their native environment and behave so also in the coastal habitat. They are dormant in winter on the coast, even though growing conditions are favorable. In the foothills, however, alpine races grow taller than they do in their own environment.

Studies of variability in *Potentilla glandulosa* were extended by intercrossing races (Clausen *et al.*, 1947; Clausen, 1949). The F_1 hybrids were both fertile and vigorous. Among 1000 F_2 plants from one cross, and 578 from another, no two plants looked alike. In one experiment the 578 F_2 hybrids were clonally propagated in each of three zones—coastal, foothills, and high Sierras—for studies of fitness. Plant responses in the three environments were "more diverse than in all the wild forms of the species from the many native wild environments of western United States that were tested at the transplant stations." It is significant that a great number of adaptive races can arise by recombination of the genes carried in but two ecotypes.

Polyploidy may result in the development of new ecotypes and in a general extension of the ecologic range of plants. Gregor and Sansome (1930) and Gregor (1931) cited evidence that common timothy (*Phleum pratense* ($6\ n = 42$)) has a much wider adaptation then its probable progenitors, *p. pratense* var. *nodosum* ($2\ n = 14$), adapted to dry, uncultivated low-elevation areas, and *P. alpinum* ($4\ n = 28$), found in moist situations at high altitudes. As was shown by Evans *et al.* (1935) in studies over a considerable range of latitude, many races or ecotypes of timothy now exist, differing in their temperature and light requirements for normal growth and reproduction.

One more general aspect of the ecologic effects of polyploidy has been discussed by Clausen *et al.* (1945). They have pointed out that amphiploids are more likely to differ from their diploid ancestors in their ecological requirements than are autoploids.

In summary of the ecotype concept, it has been noted that natural populations of a species occur in places favorable for survival. Among the many hereditary variants, some possess potential survival value for particular environments. Other variations appear to have no survival value and represent chance differences which do not interfere with the requirements for existence.

Differences occur between any two populations from the same environment, but in comparing one population with another from different climates, differences of larger magnitude may be found. Ecologic races are not homogeneous, and the biotypes within an ecotype may vary in ability to live in another climate zone.

Ecotypes differ in their degree of tolerance to environmental changes. When two are hybridized, many new recombinations of characteristics and capacities for survival in diverse environments may result. Thus new ecologic races can arise.

A critical point has been raised by Stebbins (1950). He asks, "To what extent are the different biotypes of a species grouped into partly discontinuous groups which may be recognized as ecotypes, and to what extent do they form a continuous series?" Some data on this point are available. Variation in *Pinus sylvestris* has been shown by Engler, Burger, and others (cited by Stebbins, 1950), to be of the continuous type. This was noted also in *Plantago maritima* by Gregor *et al.* (1936). It would be logical to assume that in nature both the tendency to evolve partly discontinuous groups (ecotypes) and the tendency to evolve more or less continuous series are possible. If a species is found in a number of sharply contrasting environments, clearly defined ecotypes may be present, whereas the variability of a species, occurring throughout an extensive area in which climatic changes are gradual, may be of the more continuous type.

2. *The Origin of Crop Plants*

During the period from 1920 to 1939, Vavilov (1951) directed the enormous task of collecting thousands of varieties of crop plants for possible use in the U. S. S. R. The geographic survey made possible by studies of these world collections was so extensive and at the same time so thorough that it has never been equalled. In his determination of "centers of origin" of crop plants, Vavilov used what he called the "differential phyto-geographic method." One of the most important features of this method was a detailed study of the racial composition of botanical varieties and species and a study of the geographic distribution of *all* of their diversity. Additional evidence of origin was obtained through studies of cytological behavior, hybridization, and disease reactions.

a. Primary Centers of Origin. On the basis of studies of the extensive world collections of plant materials. Vavilov (1926, 1951) recognized the following eight centers of probable origin of crop plants:

1. Chinese center—including mountainous regions of central and western China, with adjacent lowlands.

2. Indian center—including Burma and Assam, but excluding northwest India.

3. *Central Asiatic center*—including northwest India, Afghanistan, Tadjikistan, Uzbekistan, and western Tian-Shan.

4. *Near-Eastern center*—including interior Asia Minor, Transcaucasia, Iran, and Turkmenistan.

5. *Mediterranean center*—including areas bordering Mediterranean Sea.

6. *Abyssinian center*—Ethiopia and the hill country of Eritrea.

7. *South Mexican and Central American center*—including the Antilles.

8. *South American (Ecuadorean-Bolivian-Peruvian) center.* Two subcenters include Chiloe island and Brazil.

Of more than 600 important cultivated crop plants, only 100 are of New World origin. Approximately 400 came from the mountains and tropical regions of southern Asia. It was suggested further by Vavilov that large centers of origin, or "gene centers," could be broken up into smaller centers of "agro-ecological groups." This idea has been extended by Harlan (1951), who believes that even Vavilov's agroecological groups can be divided still further into gene microcenters, some of which are extremely active from the evolutionary viewpoint. For example, in Turkish Thrace, a typical wheat field may be composed of a grand mixture of forms, including several species, many botanical varieties, and dozens of agronomic varieties. In addition, around the borders of the field, one may find several wild relatives such as *Haynaldia* and *Aegilops.* These complex mixtures of variant forms do not appear to be the result of simple mechanical mixtures but rather of active interbreeding among the various populations. A similar situation in Armenia and Georgia (U.S.S.R.) was described by Vavilov (1951). Active evolution was apparent in a number of tree fruits as well as in wheat and alfalfa.

b. Range of Diversity in Crop Plants. Throughout his study of the world collections of crop plants, Vavilov was impressed with the great diversity of forms. He found that all Linnean species were composed of subspecies and varieties, and varieties in turn were composed of many races differing in morphological and physiological characters. The diversity of wheat, for example, was found to be immense, with at least 400 heritable morphological and physiological characters, most of which can freely combine in all directions. Even in rye, hundreds of forms were distinguished, originating mainly in the regions of Trans-Caucasus, Iran, and Afghanistan. Wild species were found to be just as variable as cultivated ones, wild clovers, alfalfa, timothy, wild oats, and others showing the same kind of diversity as was found in wheat or rye. Polymorphism appeared to be similar in both cross-pollinated and self-pollinated crops. Parallel variation appeared to be common, furnishing confirmation for the "Law of Homologous Series in Heritable Variation" first proposed in 1920 (Vavilov, 1922).

IV. Climatic Factors Affecting Crop Adaptation

In dividing the world into a number of "climatic types" there is a certain artificiality in the establishment of their boundaries. This is because boundaries appear to be sharp delineations, whereas actually there is a gradual transition in the climate. In comparing different climates, therefore, attention should be focused on the interiors of climatic regions rather than their boundaries.

For a climatic classification to be realistic, boundaries should conform more or less to known plant distribution boundaries. Köppen (1931) attempted to do this, and although some objections were raised by Thornthwaite (1943) because of the plant classification used, the Köppen system of climatic classification represents the one most widely accepted today. Köppen determined the divisions of his classification mainly on the basis of monthly temperature and precipitation data. The main groups, with certain subgroups, are given below.

A—Tropical rainy climates. Temperature of coolest month over 64.4° F. (18° C.), winterless regions with adequate rainfall. Subgroups include the tropical rain forest climate, Af, where there is no distinctly dry season, and the periodically dry savanna climate, Aw, where at least ten times as much rain falls in the wettest month of summer as in the driest month of winter.

B—Dry climates, where evaporation exceeds precipitation, including the steppe climate, BS, and the deserts, BW.

C—Humid mesothermal climates. Coldest month between 64.4° F. (18° C.) and 32° F. (0° C.), with winters mild and short. Subgroups include the humid subtropical type, Cw, with warm climate and dry winters, Cf, with warm climate and no dry season, and Cs, the Mediterranean or dry summer subtropical type.

D—Humid microthermal climates. Temperature of coldest month under 32° F. (0° C.) and warmest month over 50° F. (10° C.). Winters are severe and long. Regions of cold dry winters where at least ten times as much rain falls in the wettest month of summer as in the driest month of winter are classified Dw. If no distinctly dry season is present, the type is Df.

E—Polar climates, with temperature of warmest month under 50° F. (10° C.).

The climate near the ground and that several feet above the ground are not the same. The earth's surface, as the lower limit of the atmosphere, plays an important role in meteorology. The heating and cooling of the atmosphere in the course of a day and according to seasons takes place largely through the soil surface. Close to the ground, great climatic differences can be found because of the modifying influences exerted by the soil and the plant cover. Geiger (1950) has defined the expression "near the ground" as being within 2 m. of the surface, and the climate in this location is known as the plant climate or microclimate. Most weather instruments are placed approximately 1.5 to 2 m. from the ground in order to escape the extreme variability of the microclimate. Data from such locations are useful in describing conditions of larger areas and are the kind used in climatic classifications.

1. The Moisture Factor

Practically all of the precipitation of the earth is the result of adiabatic cooling of ascending air masses. Trewartha (1943) has listed the following factors which determine the distribution of precipitation over the earth: (1) regions or belts of converging air flow, (2) the character of the moisture-bearing winds, (3) the air temperature, which influences the water-holding capacity of the air, (4) the distance from oceans, and (5) the presence of highland or mountain areas.

a. Precipitation Patterns. The pattern of precipitation is highly important in determining crop adaptation. World precipitation patterns have been described by Brooks (1935), Byers (1937), Humphreys (1941), Petterssen (1941), Kendrew (1942), and Trewartha (1943). A classification similar to Kendrew's is as follows:

1. Equatorial—two seasons of heaviest rain during the year occurring about the time the sun is overhead; intervening months much less rainy, but with no pronounced dry season. Occurs only near the Equator, but does not occur in all areas within that region.

2. Tropical—between the zone of (1) and the Tropics of Cancer and Capricorn; most rain during the hottest months when the sun is highest with winter a pronounced dry season. May be subdivided into: (*a*) with two maxima of monthly rainfall, occurring in latitudes out to 15° to 20°, with drought prevailing in winter, and (*b*) with a single maximum rainfall, and the dry season much longer.

3. Monsoon—with a pronounced maximum in summer, and a long dry season; occurs both inside and outside the tropics, especially on east coasts of continents.

4. Mediterranean—most rain in the winter six months, with summers dry. Likely to occur along western sides of land masses in transition zone between prevailing westerlies and subtropical highs, at latitudes of 30° to 40°.

5. Continental interiors—in temperate latitudes, most rain in summer or late spring, and winters much less rainy but not rainless. Less periodicity than in monsoon or Mediterranean types.

6. West coasts of continents—poleward from 40°, usually abundant rain in all seasons, with the maximum in autumn or winter. Mountains cause an increase in rainfall. In addition, east coasts of continents, although on the leeward side of prevailing westerlies, are inclined to be humid.

7. Polar—because of low temperatures and low absolute humidity, precipitation is low. Similar to continental interiors where maximum occurs in the warm season, but total is very low.

In addition to the pattern of precipitation, the nature of the precipitation also is important. Rain may be of the thunderstorm type, generally falling in heavy showers during the hottest part of the day, or of the cyclonic type, falling irrespective of time of day, less heavy, but often of longer duration. In the thunderstorm type, greater amounts of runoff are expected because of the higher intensities.

b. Precipitation Effectiveness and Humidity Provinces. Numerous methods for defining and using precipitation effectiveness for the delineation of humidity provinces have been described. Losses of moisture due to evaporation, runoff, and percolation need to be known. Since few of these factors have been measured extensively, only those available over large areas have been used in defining precipitation effectiveness.

(*1*) *Precipitation-evaporation ratio.* Transeau (1905) suggested that the ratio of total annual precipitation to total annual evaporation be used as an index of precipitation effectiveness. Penck (1910) used a similar method in his classification of climates. The use of any method involving evaporation is limited, however, because evaporation data are not available from many weather stations.

Meyer (1926) developed a precipitation-saturation deficit quotient by dividing the annual precipitation in millimeters by the absolute saturation deficit of the air, expressed in millimeters of mercury. He recognized the fact that this did not directly take into account the effect of wind on the saturation deficit. Additional expressions of a similar nature were developed by Szymiekwicz (1925) and Trumble (1937).

In 1933 Isozoki (cited by Thornthwaite, 1948) computed ratios for stations in Japan, using average annual precipitation and annual evaporation from pans. Trumble (1939), using pan evaporation data, derived an empirical equation relating monthly evaporation to vapor pressure deficit, which he computed from temperature values. He determined that the water need for a month exceeds the water supply when computed evaporation is more than three times the precipitation.

(*2*) *Lang's rain factor.* Lang (cited by Klages, 1942) used a rain factor obtained by dividing the annual precipitation in millimeters by the mean annual temperature in degrees Centigrade. This index is commonly called the P-T ratio, and was used to classify climates. Klages pointed out that saturation deficit usually provides a more reliable index of the combined effect of all the factors involved in determining rates of evaporation than does temperature. Meyer's ratio would appear to give a truer picture of existing humidity conditions than Lang's P-T quotients.

Lang's quotient was modified slightly by De Martonne (1926) and given an index of aridity. This index was used by Andrews and Maze (1933) in Australia, and by Perrin (1931), who pointed out that it did not apply well to cool zones.

(*3*) *Precipitation effectiveness index.* Thornthwaite (1931, 1933) developed an empirical formula for expressing the precipitation-evaporation ratio. He recognized the weakness of using annual values and computed his P-E index or monthly data:

$$\text{P-E Index} = \sum_{n=1}^{12} 10\left(\frac{P}{E}\right) n.$$

If evaporation data were not available, a formula based on mean monthly temperature and precipitation values was used. Thornthwaite stated that although such factors as vapor tension, wind, and pressure had not been taken into consideration, the resulting error was small. Foster (1948) noted a close relationship between vapor pressure and temperature—a fact which may account for the small differences mentioned by Thornthwaite. He pointed out that evaporation, at least from an open pan, is related to humidity and wind movement. Thornthwaite's formula for the index based on mean monthly precipitation in inches and temperatures in degrees Fahrenheit is:

$$\text{P-E Index} = \sum_{n=1}^{12} 115\left(\frac{P}{T-10}\right)^{10/9} n.$$

(*4*) *Potential evapotranspiration moisture index.* As a further method of measuring precipitation effectiveness, Thornthwaite (1948) developed the potential evapotranspiration concept of water needs. Actual evapotranspiration refers to the water lost through evaporation and transportation, which depends on climate, soil moisture supply, plant cover, and land management. Potential evapotranspiration, however, represents the transfer of water to the atmosphere that would be possible under conditions of full vegetative cover and ideal moisture supply. This value, according to Thornthwaite, depends only on the climate but is normally a value extremely difficult to determine.

Experimentally, through the use of especially designed evapotranspirometers, potential evapotranspiration has been measured. The principle is to keep a vegetation-covered area supplied with water by subirrigation and to measure daily water use. Thornthwaite found that where adjustments were made for variations in day length, there was a close relationship between mean monthly temperature and potential evapotranspiration. On this basis he developed a formula for computing water loss, using only latitude and temperature data.

Rainfall may be less than water needs during certain periods of the year. When excess water is available, some of it is stored in the soil, the amount and its availability to plants varying with soil texture and the nature of the root system. The ratio between precipitation and potential evapotranspiration is used to determine whether a climate is moist or dry. As water deficiency increases, with respect to water need, the climate becomes arid; as water surplus becomes larger, the climate is more humid. In his generalized moisture index, Thornthwaite gives more weight to water surpluses than to water deficiencies. This is because soil moisture stored in a period of surplus tends to counteract a deficiency at a later period.

Sanderson (1950) found that the Thornthwaite formula for computing potential evapotranspiration appeared to be valid for the latitude of Toronto, Canada, for both vegetation-covered and moist soil. Daily and even monthly measured values did not always agree with computed values, but the formula did not consistently overestimate nor underestimate evapotranspiration for specific months of the year. Thornthwaite has used computed values in obtaining a measure of soil tractionability for northern areas, and Sanderson's results indicate a sufficiently satisfactory agreement to justify this. He has also used his empirical relations, derived from middle latitude data, to compute potential evapotranspiration in the tropics (1951), but points out that this must be done with caution. McCloud (unpublished data) found that in Florida computed values underestimated water loss, particularly at mean temperatures above 75° F.

c. Transpiration and Wilting of Plants. All plants require water for their existence and development. In most species, a large part of this water takes no permanent part in the development or metabolic processes of the plant; but is lost through transpiration. Such losses have been estimated to be as high as 99 per cent of the water that enters the plant. Although transpiration does exert a cooling effect on the plant, this effect tends to be obscured by irradiation and convection. Small amounts of water are used in hydration of the cells, chemical combination, and maintenance of turgor pressure and in transportation of materials within the plant.

As noted by Klages (1942), different species may show different transpiration ratios when grown under the same conditions. Millets, sorghums, and corn are among the most efficient of crop plants in the use of water. Transpiration ratios, however, are of value only if the environmental conditions are specified. From the results of many investigations on the use of water by plants, including those of Widtsoe (1909), Briggs and Shantz (1912a, 1912b, 1913, 1914), Kiesselbach (1915), Shantz and Piemeisel (1927), Richardson and Trumble (1928), and others, certain generalizations appear justified. In wet climates the efficiency of transpiration may be much greater than in dry climates. Efficiency of transpiration may be lowered by infertile soil, by soil too dry or too wet, by high evaporative power of the air, or by invasion by parasitic fungi. There is no evidence that transpiration efficiency is related to drought resistance.

Plants may wilt if transpiration continues to be greater than the uptake of water, and if soil moisture is depleted sufficiently, the permanent wilting percentage is reached. This point is defined as the percentage of water in the soil when plants growing in it have just reached a condition of permanent wilting (Briggs and Shantz, 1912a). Later (1912b) these workers showed that hydrophytes, mesophytes, and xerophytes all reduce the water content of a given type of soil to about the same value, before the condition of permanent wilting is reached. This principle has been confirmed by the extensive investigations of Veihmeyer and Hendrickson (1938, 1948, 1950). Soil texture appears to be the primary factor in determining permanent wilting percentage, values of which may range from 1 per cent in sands to more than 20 per cent in certain compact clays.

d. Drought and Excess Moisture. A water deficit in the plant may be caused by hot dry winds, creating atmospheric drought, or by a scarcity of available soil moisture, resulting in soil drought. We usually think of drought in terms of moisture deficiencies deviating sufficiently from the normal condition to seriously reduce crop yields. Barger and Thom (1949a) measured drought intensity on the basis of the minimal amounts of rainfall that will just permit normal development of the corn plant during specified time intervals. Correlations between maximum rainfall deficits and deviations of county corn yields in Iowa, for years in which drought conditions occurred, indicated that from

25 to 60 per cent of the total variability in yield was explained by this criterion. For different areas (1949b) they determined the probability of occurrence of different amounts of rainfall for periods of different duration.

In North Carolina, van Bavel (1953) proposed that the incidence of drought be characterized by determining for a particular crop the number of drought-days to which it is subjected. For tobacco, at Raleigh, it was estimated that the average number of drought-days from May 15 to August 27 is 31, and that there is an 80 per cent chance of having at least 20 drought-days each summer. The root zone was estimated to be 8 in. for tobacco, and for deeper rooted crops the incidence of drought-days in those soils studied would be somewhat less.

Frequency of drought is an important climatic factor affecting the choice of crops as well as the level of and variability in their production. With limited rainfall, for example, alfalfa has been shown to deplete subsoil moisture to great depths, and several years of fallowing may be required to restore them (Kiesselbach *et al.,* 1929, 1934; Myers, 1936). Corn has certain critical periods, one particularly at time of silking and tasseling. Sorghum, in contrast, tends to stop growing if moisture is not available and remains quiescent until conditions are again favorable. Root systems of sorghum have more secondary roots per unit area than are found on corn, making it better adapted to drier conditions. Farm practices used to lessen drought hazards, include fallowing, most effective in areas of winter and early spring rains, and the growing of early-maturing varieties to escape the worst effects of drought.

Too much moisture may be detrimental, just as too little moisture. One of the most pronounced effects of too much water is poor nitrification, often noticeable in the yellowed appearance of corn on heavy or poorly drained soils in the corn belt during May or June. Other effects of too much moisture include late and nonuniform maturity and poor quality of seed. For such reasons, grain sorghums cannot be produced successfully in the more humid areas of the corn belt, whereas they are quite successful under the more arid conditions of western Nebraska, Kansas, and Oklahoma.

e. Irrigation. Where water is available at reasonable cost, irrigation permits a control of crop production not otherwise possible. Soil moisture can be maintained at the optimal level for growth and can be regulated for the best development and maturity of the crop. As suggested by Thorne and Peterson (1949), irrigation should be considered as a supplemental supply of water to be used where natural precipitation is inadequate. Every effort should be exerted to make full and effective use of the natural rainfall.

At the present time there are more than 21 million acres of irrigated land in the western half of the United States. According to estimates by the Bureau of Reclamation, this acreage may eventually be expanded to approximately 38 million (Parks, 1951). In addition, there is a growing interest in irrigation in the midwestern and eastern states, and where water is readily available, a considerable increase in the acreage irrigated in these regions is to be expected.

In the tropics irrigation is often necessary where annual rainfall is high but where its periodicity is such that dry seasons occur regularly each year. In arid regions having less than 10 in. of annual precipitation, irrigation is essential to agriculture. With 20 in. or less of annual rainfall, it may be necessary for certain intensively cultivated crops but may not be essential for small grain culture. In subhumid and humid regions, rainfall may be sufficient for most crops in most years, but for highest yields with such crops as potatoes and other vegetables, irrigation may be profitable.

Thornthwaite (1948) has pointed out a number of areas in the humid southeastern part of the United States which have a high annual rainfall but which are subject to frequent and severe droughts of such intensity as to cut crop production rather regularly. Possibilities for irrigation in the Southeast have been discussed by Camp (1949) and Nettles *et al.* (1952).

Soil properties may greatly affect irrigation practices. If soils are highly permeable, they are difficult to irrigate because of rapid percolation. Impermeable soils transmit water rapidly over the surface but are difficult to wet thoroughly. The amount of water that can be stored by the soil for periods between irrigations is influenced by the size of soil particles, compactness and depth of the soil, organic matter content, and the level of ground water.

In arid regions, in addition to physical properties of the soil, the chemical composition also is of great importance. Salts may be present in undesirable quantities and may be brought in by the irrigation water as well. According to Thorne and Peterson (1949), three kinds of soils are found in the western irrigation areas, all of which present problems in management. These include: (1) saline soils with sufficient soluble salts to interfere with crop growth, the principal anions being chloride, sulfate, nitrate, and some bicarbonate; (2) saline-alkali soils containing sufficient exchangeable sodium to interfere with plant growth and also appreciable amounts of soluble salts; and (3) nonsaline alkali soils which contain high exchangeable sodium but which are low in soluble salts.

The salt content of the surface layers of soil may fluctuate considerably. In dry weather salts tend to concentrate at the surface, whereas in wet weather they tend to leach downward temporarily. Even if the irrigation water is free from salts, they may still accumulate at the surface. Drainage may be a possible answer in some areas. According to Davis (1948), in the Imperial Valley, California, the water from the Colorado river brings in 4.25 tons of salts to each cultivated acre each year. Alkali spots develop in a few years, and although this may or may not be a permanent solution of the problem, flooding soils for three to six weeks during the cool season helps to reduce salt concentration in the surface soil.

The Salt River Valley of Arizona has faced serious problems. The soil texture has changed considerably since irrigation was started. In 1899, a survey showed that 21 per cent of the soils in the valley were clays or clay loams. A second survey twenty-eight years later showed that 82 per cent of the soils were these fine-textured types. In recent years efforts have been made to remove much of the silt in the irrigation water before it goes into the irrigation system. Adequate drainage has helped in keeping down the concentration of salts in the upper soil layers.

Another hazard to irrigation agriculture in the arid West is the destruction of watersheds. The invasion of watershed areas, with the accompanying construction of dams, diversion works, mine shafts, cutting of timber, grazing by cattle and sheep, and building of roads, has resulted in a change in stream-flow characteristics and in an unbalance in physical and biological features of the original area.

Most irrigated areas in the West have not been in operation long enough to determine how permanent they will be. In Hawaii, however, sugar cane has been grown on some irrigated lands for nearly a century. No crop rotation has been practiced and yields today are higher than they were 50 years ago.

One of the oldest continuous rotation experiments under irrigation in North America is located at Lethbridge, Alberta (Palmer, 1949). A ten-year rotation of alfalfa six years, oats, barley, sugar beets, and spring wheat has been practiced for more than 40 years. The soil is a rich prairie soil, fertilized liberally with phosphate and manure. From 1937 to 1946 the average yield of oats was 109 bu.; barley, 70 bu.; sugar beets, 18 tons; and wheat, 59 bu. per acre. Organic matter has decreased somewhat, but the level of nitrogen in the soil has been maintained.

In the humid regions, many experiments have shown profitable increases in yields of potatoes, corn, and other crops by supplemental irrigation. Others have shown little or no increases. The determination of whether or not it is profitable to irrigate in humid areas will depend largely on the availability of water and the cost of developing and maintaining the irrigation system, as well as on the drought frequency and intensity.

2. The Temperature Factor

a. General Patterns. Air temperatures result from insolation (exposure to solar rays). Because both latitude and season affect the amount of heat received from the sun, temperatures vary greatly from place to place. In Köppen's classification, four major temperature divisions, tropical, mesothermal, microthermal, and polar, are used. These are subdivided further in order to define regional temperature conditions. Additional useful information include mean monthly temperatures as well as the mean daily maximum and mean daily minimum for each month. The annual range of temperature, between the warmest and coldest months, may indicate whether the climate is of a continental or a marine type. The difference between the maximum and minimum temperatures, the diurnal range, also indicates the variability to which plant life is subjected. Both the diurnal and annual range depend largely on the proximity to large bodies of water and on the humidity of the atmosphere. The annual range of temperature is also influenced greatly by latitude. In regions near the Equator the diurnal range is considerably greater than the annual range (Kendrew, 1942).

Hopkins (1938) established bioclimatic zones, which recognized the effects of oceanic, continental, and physiographic features on temperature and life zones in general. In terms of a periodic event in plant activity, his Bioclimatic Law stated that for each degree of latitude north to south, each decrease of 400 ft. in altitude, or each 5° of longitude west to east, the event will occur, on the average, four days earlier. Evans (1931) showed that in relation to the time of blooming of timothy, Hopkins' law did not give proper emphasis to the gradually increasing length of day from southern to northern latitudes. The blooming of timothy progressed at constantly accelerated rates rather than at a uniform constant rate. Kendrew (1942) has pointed out that elevation also affects mean temperature. For each increase of 300 ft. in elevation, the mean temperature is 1° F. cooler.

b. Measures of Thermal Efficiency. (*1*) *Length of the growing season.* The length of the growing season is defined as the length of interval in days between the last killing frost in the spring and the first in the fall. The recording of a "killing frost" depends somewhat upon the vegetation in the vicinity of the observer. For this reason it would appear more logical to use the occurrence of certain specific temperatures. Shaw *et al.* (1954) have presented maps of Iowa of the occurrence of 32°, 28°, 24°, and 16° F. A disadvantage of using an instrument shelter temperature is that it does not represent the plant temperature. Waggoner and Shaw (1952) and Shaw (unpublished data) found that on cloudy nights leaf temperatures approximated instrument shelter temperatures, whereas on clear nights leaves may be as much as 8.0° cooler. When air temperatures at 4.5 ft. were 32° F., leaves near the ground registered 24° F.

The length of the growing season is variable from year to year. On the basis of large-scale topographic features, the growing season generally increases in length from north to south in the northern hemisphere (Kincer, 1941) and decreases in length with increasing altitude. On a more local basis, particularly in flat areas, as well as in many mountain valleys, the phenomenon of temperature inversion may upset this relationship. Under certain conditions, low areas tend to become cold spots, because of cold air accumulating there from air drainage.

The use of the length of the frost-free period excludes certain other environmental factors and is determined strictly by prevailing temperature conditions. Klages (1942) has noted that it expresses what should be called the thermal growing season and is really not a temperature efficiency index. It deals only with the interval between the last killing frost in the spring and the first in the fall, and gives no measure of temperature intensities in the intervening interval. However, it does show high correlation with more complex temperature evaluations.

(*2*) *Exponential index.* Livingston and Livingston (1913) computed thermal efficiency on the basis of the principle of van't Hoff and Arrhenius, which stated that the velocity of chemical reactions doubles with each increase of approximately 10° C. Their efficiency index for each day of the growing season was computed from the formula

$$u = 2\left(\frac{t - 40}{18}\right).$$

This index recognizes that plant responses to increasing temperature are not linear, but it tends to give too high an efficiency to supraoptimal temperatures.

(*3*) *Temperature summation or degree days.* The direct summation of temperatures above a certain zero or vital temperature point gives a measure of temperature efficiency. This method, however, gives no weighing of efficiency to different temperatures, and detrimental effects of supraoptimal temperatures are ignored. Used rather extensively in the canning industry (also called the heat unit system, or growing degree days), this method has been found useful in arranging planting schedules to allow an even flow of the crop into the cannery at harvest time. Its application, especially in the production of canning peas and sweet corn, has been discussed by Barnard (1948), Bomalaski (1948), Phillips (1950), Lana and Haber (1951), and Katz (1952).

Variability in the number of heat units required to grow a crop to a certain stage of maturity was considerable from year to year, cool seasons showing a lower, and warm seasons a higher, requirement. More extensive and more accurate climatological data and especially temperatures of the actual plant climate are needed. An improvement in this method was suggested by Decker (1953), who developed a formula giving each temperature an efficiency rating.

(*4*) *Thornthwaite's temperature efficiency index.* Thornthwaite (1931) evaluated the effects of temperature on a linear basis. His index involves a linear transformation of the remainder method and is computed using the formula

$$I = \sum_{n=1}^{12} \left(\frac{T - 32}{4}\right) n$$

where I is made up of the sum of the 12 monthly indices and T is the mean monthly temperature in degrees Fahrenheit. On the basis of this index, six provinces of temperature efficiency were differentiated. Summer concentration of heat was expressed as the ratio of the accumulation for the three summer months to the total annual thermal efficiency. Latitude, length of day, and distance from the ocean all affect this value of summer concentration.

A new thermal efficiency index, based on potential evapotranspiration, has been developed by Thornthwaite (1948). Since temperature is the primary variable used in computing evapotranspiration, this index is largely a function of temperature.

(*5*) *Physiological index.* The physiological temperature index is based on the work of Lehenbauer (1914), who determined rates of elongation of maize shoots. This index takes into account the effect of supraoptimal temperatures. Livingston (1916) and Pearson (1924, 1931) have pointed out the advantages of this system, and Livingston has also summarized the disadvantages. It is based on temperature-growth relations of a single plant species, and on the growth of plants as seedlings only. Measurements were made of shoot elongation only, with constant temperatures for 12-hour periods. The effects of natural temperature fluctuations at different stages of growth probably are important, and place severe restrictions on the use of the index.

(*6*) *Moisture-temperature or hydrothermal index.* Livingston (1916) developed a moisture-temperature efficiency index using the formula

$$I_{mt} = I_t \frac{I_p}{I_e},$$

where I_{mt} is the moisture-temperature index, I_t is the index of temperature evaluated on the basis of the physiological index, and I_p and I_e represent the indices of precipitation intensity and atmospheric evaporating power. This index assumes that plant growth increases proportionally to the value of the rainfall index, is retarded proportionally to the index of evaporation, and that the temperature index is correlated with the rates of activity manifested in the plants.

(*7*) *Sunlight degrees.* Clements (1940, 1951) developed a method which is based on sunlight intensity and its absorption. Two distant recording thermographs were used, one with the "bulb" painted white and placed inside a regular weather shelter, the other with the "bulb" painted black and exposed to direct sunlight. The white-bulb instrument recorded the air temperature, and the black bulb was heated by the sun's rays. From differences between the recorded temperatures of the two instruments, a measure of light intensity was computed and expressed as "sunlight degrees." Marked differences in the yield of sugar cane at two locations, similar in fertilizer, moisture, and temperature conditions, were explained on the basis of differences in sunlight intensity.

c. Temperature and Plant Growth. (*1*) *Cardinal growth temperatures.* As noted by Klages (1942), plant activities occur within certain more or less defined tolerance limits. The requirements of life must be present in a minimal amount in order for the plant to function. At a certain level of these requirements the plant will function at its optimum rate, whereas at still higher levels the plant will cease to function. These levels, minimum, optimum, and maximum, are called the cardinal points. For each factor of a plant's environment, there are cardinal points, but as Pfeffer (1903) and others have pointed out, it may be impossible to determine them with accuracy because of the interaction of different plant and environmental factors.

The determination of cardinal points of growth with respect to any environmental factor is of practical value only when correlated with a particular developmental stage in the life rhythm of the plant (Klages, 1942). These values differ among species and within species at different stages of development (see Section II, 1.c).

(*2*) *Effect of low temperature.* Injury to plants as a result of low temperature may occur because of desiccation, chilling, or freezing.

In many plant species, injury is caused by chilling, particularly in plants native to tropical or subtropical regions. Sellschop and Salmon (1928) found that exposure to a temperature of 0.5° to 5.0° C. for 24 to 36 hours was injurious to rice, cotton, and peanuts, but that soybeans, tomatoes, and flax showed no injury. The reason probably lies in disturbances in the metabolic activities and physiological conditions within the cells (Meyer and Anderson, 1952).

Plants subjected to freezing temperatures usually are injured because of the formation of ice crystals. As shown by Simonovitch and Scarth (1938) and Stuckey and Curtis (1938), small ice crystals formed within the living cells injure the cytoplasm by their lacerating effect, apparently disorganizing the protoplasmic structure and resulting in death of the cells. Ice crystals that form in the intercellular spaces tend to withdraw water from the cells and dehydrate the protoplasm. Both intracellular and intercellular ice formation occurred in freezing experiments with red cabbage (Simonovitch and Scarth, 1938).

Winter injury of perennial legumes often occurs on flat and depressed areas where ice sheets cover the plants and interfere with normal respiration. Another type of injury is heaving, mainly a physical process caused by alternate freezing and thawing, which results in the plants being lifted out of the soil.

Winterhardiness is of great importance in the higher latitudes, and plant breeders have searched for criteria by which this characteristic could be expressed or predicted. Klages (1926) concluded that the most hardy varieties of winter wheat had comparatively small leaf areas. In alfalfa, it is well known that certain extremely hardy varieties, such as LADAK, exhibit a low, rosette type of growth in the fall, whereas the nonhardy southern common varieties have an erect fall growth habit.

(3) *Effect of high temperature.* The injurious effect of high temperature may be due to desiccation of plant tissues, metabolic disturbances, or direct thermal effects on the protoplasm (Meyer and Anderson, 1952).

The temperatures of the upper surfaces of leaves depend upon atmospheric conditions, especially cloud cover. Under a clear sky leaves exposed to radiation are warmer than the air, but on cloudy days these leaves are slightly cooler than air temperature (Curtiss, 1936; Waggoner and Shaw, 1952).

Although growth may cease at the maximum temperature for a given species, death may not result unless this temperature continues for some time. Heat damage to crops often is caused by the combined effects of high temperature and drouth. Hot winds may greatly accelerate the damage because of the resulting rapid increase in transpiration rate.

(*4*) *Thermoperiodicity*. Although in some plants the growth rate may be rather constant from day to night, in others the greater part of stem elongation occurs during the night. For such plants it is likely that there will be different optimal temperatures during day and night. Experiments by Went (1944, 1945, 1948, 1950) have shown that young tomato seedlings grow best at 26° to 30° C. As the plant grows older the optimal night temperature drops, passing through 23° and 20° C. and finally reaching 13° to 18° C. for different varieties. Rubber formation in guayule (*Parthenium argentatum*) was found by Bonner (1944) to proceed at the fastest rate at night temperatures between 5° and 10° C. and to be very slight above 15° C. The Valencia peanut (*Arachis hypogaea*) grows best with relatively high day and night temperatures. For both growth and gynophore development optimal temperatures were 26° C. days and 27° C. nights (Jacobs, 1951).

3. The Light Factor

Light is an important factor in determining the distribution of plants. Through the photosynthetic process, radiant energy from the sun is converted by green plants into chemical energy. The visible spectrum includes wavelengths extending from approximately 7500 to 4000 Ångström units, the range most important in photosynthesis. As noted by Shirley (1945), the energy in the wavelengths of visible light makes up approximately 50 per cent of the total solar energy. In photosynthesis, it has been shown by Pfeiffer (1928) and Shirley (1929) that the full solar spectrum, or at least the visible light plus the ultraviolet, is more effective than the visible spectrum alone. Most green plants grow normally only when exposed to light having most of the wavelengths of visible light, but as shown by Hoover (1937) and others peaks of absorption in photosynthesis occur in the violet-blue and orange-red regions.

a. Light Intensity. The characteristics of light that are of importance in adaptation studies include total intensity, duration, and quality. In the production of ordinary crops, intensity of light has hardly been considered a limiting factor, but it may be of great importance. Light intensity increases with elevation, mountain tops 10,000 ft. above sea level being exposed to 1000 ft.-c. brighter light than is present at sea level. Humid climates have lower light intensity than dry climates. Coastal cloudy, or foggy areas and tropical mountainous regions are known to have such a low light intensity as to markedly affect plant behavior. Latitude is important in determining the angle of the solar rays as they strike the earth surface. For this reason light intensity is greatest at the Equator and decreases progressively toward the poles.

The effects of light intensity on the rate of photosynthesis have been studied with many plants. Hoover *et al.* (1933) showed that in wheat the rate is approximately proportional to light intensity, providing that carbon dioxode is not a limiting factor.

In sugar-cane production in Hawaii it has been shown by Clements (1940) that sunlight intensity greatly affects final yield (see Section IV, 2.b.7). Growth of cane was compared on two sugar plantations, Kailua, having a heavy rainfall and considerable percentage of cloudiness, and Waipio, having similar temperature conditions, but a bright, dry climate. It was found that sugar-cane plants at Waipio were receiving approximately 60 per cent more radiant energy than was available in the less sunny Kailua area. When soil, fertilizer, variety, moisture, and management conditions were similar, final yields of cane at Waipio were 134 tons per acre as compared with 65 tons at Kailua. Clements concluded that atmospheric energy was the single most important factor in determining the yield of sugar cane when lesser factors were not limiting.

In the use of companion crops for the establishment of small seeded legumes and grasses, light intensity plays an important role. Klages (1942) noted marked differences in stand and vigor of red clover and alfalfa as related to kinds and varieties of companion crops used. Light measurements showed variations from 7000 ft.-c. in a companion crop of ALASKA peas at podding stage to 1500 ft.-c. in a companion crop of MARKTON oats at time of heading. Pritchett and Nelson (1951) have shown that low light intensity may be responsible for many failures in establishing seedings of forage crops and that the choice of a companion crop that does not stool vigorously and cause undue shading is of great importance.

Light intensity may be too high as well as too low. In continental climates, especially in semiarid and arid regions, full sunlight may be detrimental to crops because of increased transpiration rates, reduced water content of the leaves, and consequent decrease in photosynthesis. Veth (cited by Shirley, 1945) gave evidence that in the tropics growth increased with an increase in light intensity only up to 20 or 30 per cent of full sunlight.

b. Photoperiodism. The length of day may be considered largely a function of latitude. At the time of the equinoxes, March 21 and September 21, the lengths of days and nights are nearly equal at all latitudes. At the beginning of summer, however, day length at 30° is 14 hours, whereas at 60° it is almost 19 hours. This difference in the comparative lengths of days and nights as related to latitude is an important factor in the natural distribution of plants.

Our present concept of the relationship between day length and the development of plants is based largely on the extensive research of Garner and Allard (1920, 1923, 1930, 1931) and Allard and Garner (1940). Somewhat earlier, Klebs (1918), who had studied the relationships of light and temperature to reproduction, stated that the process of inflorescence formation proceeded in three stages, the ripe-to-flower condition, formation of flower primordia, and development of the inflorescence itself.

In 1920, Garner and Allard reported that MARYLAND MAMMOTH tobacco always continued in a purely vegetative condition when grown out of doors at Washington, D. C., but flowered profusely when grown under short days in the greenhouse in the winter. With the coming of spring, vegetable shoots were again produced, and these continued to grow throughout the summer, without producing any flowers. Several varieties of soybeans were found to behave in a similar manner, as short-day plants. The term "photoperiod" was defined as the length of daily exposure to light, and "photoperiodism" as the response of plants to photoperiod.

Later, Garner (1933) suggested that between 12 and 14 hours, probably nearer to 14 hours, might be considered the critical photoperiod for dividing species into short-day and long-day sorts. On this basis, small grains, timothy, brome grass (*Bromus inermis*), biennial sweetclover (*Melilotus alba*), and red clover are considered long-day plants, and certain varieties of tobacco and soybeans, millet, poinsettia, chrysanthemum, Lespedeza, and hemp behave as short-day plants. Others considered "indeterminate," or day-natural, include cotton, tomato, buckwheat, and many kinds of beans.

Most plants that originated in the tropics require relatively short days and long nights for flowering, whereas many plants native to the high latitudes are long-day types. Through many generations of natural selection, species, varieties, and biotypes have developed responses to photoperiods by which they flower and fruit in definite seasons of the year.

(*1*) *Variability within species.* Within specific groups of plants great variability exists as to their photoperiodic response. In a given environmental situation, genotypes adapted to the day length of that area may soon predominate. This adaptation has been shown strikingly in studies of geographic races of side-oats grama by Olmsted (1943, 1944, 1945) and by Evans and Allard (1934) in timothy.

The native range grass, side-oats grama (*Bouteloa curtipendula*), is widely distributed over much of eastern, central, and western United States. Olmstead collected 12 strains over a latitudinal range of 17°, from Texas to North Dakota. When grown at Chicago, Illinois (42°), these strains exhibited genetic differences, particularly with respect to adaptation to photoperiod. Three strains, from southern Texas and Arizona, showed normal development and flowering behavior with a 13-hour photoperiod.

In contrast, a strain from North Dakota showed normal vegetative and flowering behavior only when given a photoperiod of 14 hours or longer. Under shorter photoperiods, tillering was abundant, internodes relatively short, and few or no flowers were produced.

Strains from more central latitudes showed variation among plants as to photoperiodic response. Those collected from Nebraska and Kansas included mainly long-day genotypes, with critical photoperiods somewhat shorter than those from North Dakota. Oklahoma and New Mexico provided strains which appeared to possess the greatest diversity in adaptation to day length. Selection among these, according to Olmsted, should offer greatest possibilities for adaptation to latitudes north or south of their own. Although Olmstead found that the 12 strains showed a slight degree of adjustment to the range of photoperiods present, in most populations some plants were able to grow well and reproduce over a rather wide range of photoperiods. This tolerance of certain genotypes probably was of little or no importance in their native environments, but it may have been of great evolutionary significance in the migration of the species to different latitudes.

Studies of 16 strains of timothy, mainly of American origin, by Evans and Allard (1934) indicated that observed earliness or lateness in flowering was due primarily to inherent differences in response to the seasonal length of day following renewal of growth in the spring. Later, Allard and Evans (1941) studied 2 American strains, MARIETTA and HURON ($6n$ types), and 3 European strains, HARPENDEN (England), MOSCOW (Russia), and WELSH s50 (all $2n$ types). Both MARIETTA and HURON were of the early type, but MARIETTA flowered in response to a 12-hour day length, whereas HURON did not flower unless the photoperiod was more than 13.5 hours.

The three European diploid strains showed the typical responses of long-day plants. They were unable to flower normally in response to the longest days (14.9 hours) at Washington, D. C., but under 16- and 18-hour days flowering occurred. A day length of 15 hours appears to be essential for flower initiation in these late strains which originated at latitudes between 50° and 60°, considerably further north than the timothy belt in the United States.

In recent studies, marked differences in photoperiodic response among varieties of other forage crops have been noted by Ludwig, Barrales, and Steppler (1953) in red clover, Wiggans in sweetclover (1953), Knight and Bennett (1953) in southern grasses, and Hanson and Sprague (1953) in northern grasses.

Among short-day species, soybeans were studied extensively by Garner and Allard (1930). Four varieties, MANDARIN, PEKING, TOKYO, and BILOXI, ranging in maturity from early to extremely late, were grown at Washington, D. C. With natural day length for that latitude, May plantings of the four varieties showed an average of 27, 56, 70, and 105 days, respectively, from germination to flowering. When the four varieties were exposed to a shorter day length, 12 hours or less, there was but a slight difference in the time required to reach the flowering stage. The time from germination to flowering was 23 days for MANDARIN, 23 days for PEKING, 24 days for TOKYO, and 27 days for BILOXI. Under normal cultivation the MANDARIN variety would appear to be adapted to relatively long days, whereas BILOXI is a distinctly short-day type. If grown near the Equator the four varieties would behave similarly as to vegetative and reproductive periods.

Corn is a plant of tropical origin, and primitive varieties in South America, Central America, and Mexico probably consisted mainly of short-day plants. Thomas (1948) found that when strains from Guatemala were subjected to a photoperiod of 11 hours at Ames, Iowa (42° north latitude), appearance of flower primordia was hastened considerably.

A study of the development and seasonal variations of the corn crop in Nebraska has recently been made by Kiesselbach (1950). The progressively longer photoperiod from south to north in Nebraska during the planting season was shown to be an important factor in the latitudinal adaptation of varieties and hybrids. Because corn is a short-day plant, standard Nebraska varieties were found to flower in 13 days less time when planted in the southern states than when grown in Nebraska. Conversely, southern varieties required 18 days longer to flower in Nebraska than in their home environment.

(2) *Importance of darkness.* From studies of the cocklebur (*Xanthium pennsylvanicum*), a short-day species, Hamner and Bonner (1938) concluded that the photoperiodic stimulus was brought about during both the light and dark periods. A continuous dark period of 8.5 to 9 hours, after a previous exposure to a favorable photoperiod, was necessary for normal flowering. The intensity, rather than the duration, of the light period was important, but the most critical factor was the absolute length of the dark period. Hamner (1944) suggested that

the length of the dark period was critical also in long-day plants, because of its inhibiting effect.

It was shown by Snyder (1940) that for long-day plants an intermittent flash lighting for 0.5 to 1 minute, followed by an equal or longer dark period, was equally as satisfactory as a continuous long day. Similar results were demonstrated also by Borthwick *et al.* (1948) through the interrupting of the middle of the dark period with usual lighting for a few minutes only.

(3) *Transition to reproductive phase.* Floral induction in many perennial forage grasses takes place in the autumn, favored by short days and low temperatures. Some of the agronomic implications, with respect to management practices, have been considered by Peterson and Loomis (1949), Metcalfe (1950), Gardner and Loomis (1953), and others.

The transition from a purely vegetative phase to a reproductive phase is marked by the differentiation of floral primordia. A minimal number of leaves must be present before this takes place, and environmental conditions favorable for initiation of flowers may be different from those promoting induction. Much progress has been made in studies of this phase of reproduction by means of micro-dissection of growing points as shown by the work of Noguchi (1929), Bonnett (1936), Evans and Grover (1940), and Sharman (1942, 1945). The approximate dates of differentiation of flower primordia in winter annuals or perennials in the spring is of considerable interest. Sass and Skogman (1951) observed that among different clones of bromegrass in the breeding nursery at Ames, Iowa, the date of first appearance of flower primordia ranged from April 4 to April 19. A few were found to be differentiated in the early autumn, but none of these survived the winter. In a warm-season grass, big bluestem (*Andropogon gerardii*), it has been shown by Holt (1952) that floral differentiation does not occur in central Iowa until the latter part of June.

During the past two decades, the literature on various phases of photoperiodism has been voluminous. Reviews of the more important contributions have been given by Garner (1937), Hamner (1944), Whyte (1946), Murneek and Whyte (1948), Borthwick *et al.* (1950), and Leopold (1951).

In view of findings in recent investigations, the classification of plants into long-day, short-day, and indeterminate categories is hardly satisfactory. In some species, these three types form a more or less continuous series and it would appear that the reactions that lead to flowering are similar in all. It would be preferable, according to Borthwick *et al.* (1950) to designate these categories according to the length of the dark period. Thus, long-day plants really are short-night plants, and short-day plants are long-night plants. This conclusion is based on the fact that a break in the middle of a 10- or 12-hour dark period prevents flowering in the BILOXI soybean or cocklebur, whereas a similar break in the middle of a 12-hour dark period promotes flowering in WINTEX winter barley and other long-day plants.

(*4*) *Mechanism of photoperiodism.* The exact mechanism of photoperiodic induction is not known. Knott (1932), Naylor (1941), and others showed that leaves are the organs through which the stimulus is received. There is some evidence by Cajlachjan (cited by Whyte, 1946) that a substance of catalytic nature, possibly a hormone, is formed in the leaves and transmitted to the meristems and other parts of the plant.

Recent investigations at Beltsville, Maryland, by Borthwick *et al.* (1948, 1950) have clearly demonstrated the importance of the quantitative aspects of light in promoting or inhibiting photoperiodic response. Using BILOXI soybean and cocklebur, both short-day plants, plants were irradiated with light of narrow wavelength bands as near the middle of the dark period as possible. The most effective light for inhibiting flowering in short-day plants or for promoting flowering in long-day plants was in the red region from 6000 A. to 6800 A.; a second less effective region was in the blue near 4000 A. A sharp limit was reached at 7200 A., and in general irradiation with the wavelength band in the infrared between 7000 A. and 7500 A. affected the short-day plants just the same as total darkness.

Further study by Borthwick *et al.* (1952) showed that this photoreaction was reversible and applied not only to floral induction but also to the control of germination in lettuce seed. Retests with the cocklebur showed that the inhibitory effect of exposure to red light in the middle of the dark period was counteracted if followed at once by exposure to infrared rays. These results, indicating that light of some colors was more effective than others, suggested that a pigment may be the absorbing agent involved in the reaction which leads to the formation of a flower-promoting substance. Recently Hendricks and Borthwick (1953) have suggested that this reversible photoreaction caused by red and infrared rays may be caused by a rearrangement of the atoms in a leaf pigment molecule.

c. Interrelations of Light and Temperature. Of all the factors of the environment that influence photoperiodic response (other than light), temperature probably is of greatest importance. From their soybean investigations, Garner and Allard (1930) concluded that variations in date of flowering of all varieties from year to year were caused primarily by temperature, even though photoperiod was responsible for one variety always being early and another variety always late in reproductive habit.

In greenhouse studies with bromegrass (*Bromus inermis*), Evans and Wilsie (1946) showed that a late flowering selection from the ACHENBACH (Kansas) variety bloomed freely only with an 18-hour or longer day, and at relatively high temperatures and high soil fertility, whereas other selections flowered over a much wider range of photoperiod, temperature, and soil fertility conditions. In central Iowa, several varieties of bromegrass of the northern and southern ecotypes often begin to flower on the same day, usually in early June. At Saskatoon, Canada, it has been noted by Knowles and White (1949) that southern varieties may flower two to four days later than northern, and usually about July 1. It is apparent that although this species is considered a long-day plant, the critical factor in determining when it blooms, especially at the higher latitudes, is the temperature.

In greenhouse work at Madison, Wisconsin, Roberts and Struckmeyer (1939) observed that red clover grew most rapidly and flowered best with long days at cool temperatures. Sweetclover responded best to long days at warm temperatures. Alfalfa grew and flowered satisfactorily under long, warm days but did not set seed if the nights were too warm.

(*1*) *Vernalization.* It has long been known that different species of plants possess different optimal requirements during several of their critical growth phases. Early work by Klebs (1918) and Gassner (1918) indicated the importance of light and temperature as related to the reproductive phase. Gassner germinated winter and spring rye at different temperatures from just above freezing to 24° C. Later, when seedlings were well established, they were transplanted into the field. The temperature during germination had no effect on flowering of spring rye, but with winter rye only the plants that were germinated at 1° to 2° C. flowered regularly and fully, regardless of date of appearance above ground in the spring. Gassner concluded that spring rye is independent of any temperature requirement for achieving the flowering stage, but winter rye must pass through a cold period either during or at some stage following germination.

Much earlier, Klippart (1858) in Ohio had observed that winter wheat could be made to behave as spring wheat by allowing seed to germinate slightly in the fall and keeping it at low temperature until planting time in the spring.

Following Gassner's earlier lead, Dolgušin and Lysenko, and Tolmačev (cited by Whyte, 1946) read papers at the All-Union Congress on Genetics in the U. S. S. R. in 1928 on pretreatment of seed with low temperature. Partially soaked and slowly germinating seeds of winter cereals were subjected to a temperature just above freezing for 15 to 60 days, the period varying with the variety. Such seed when sown in early spring produced a yield of grain the same summer, possibly even earlier than spring varieties planted at the same time. In the next few years Lysenko put out practical recommendations for treatment of seed, the process being known as "jarovizacija," which in other countries was called vernalization. The theoretical basis for vernalization was found in Lysenko's phasic development theory. The first phase was considered to be a thermal phase, high temperatures prolonging its duration. The second and later phases proceeded in succession most rapidly at higher temperatures. The specific vernalization requirement of a variety, according to Vavilov (1951), was a basic physiological character associated with its evolutionary development and related to the climate of the area of its origin.

It is now well recognized, as noted by McKinney and Sando (1933), that for the early growth stages of winter cereals, short days and low temperature are desired, whereas for flowering and seed production, long days and higher temperatures are needed. Winter cereals might well be called short-day→long-day plants or low-temperature→high-temperature plants. In contrast, spring cereals need long days and fairly high temperatures for their whole cycle of development.

Research in Great Britain by Purvis (1934, 1940, 1944) and Purvis and Gregory (1937, 1945) has refuted Lysenko's claim of an obligate thermo-phase in winter cereals for normal flowering. By exposure to short days, either with or without low temperature, flowering was achieved. Probably of still more importance was the discovery that vernalized seed could be devernalized by high-temperature treatment and that anaerobic conditions tended to inhibit vernalization. In Germany, Voss (1938) found that winter wheat would flower under continuous light, at temperatures above 20° C., if given sufficient time.

The extensive literature on vernalization, including results obtained in the United States, Canada, Australia, China, India, and other countries, is reviewed by Whyte (1946, 1948). In general, flowering was accelerated by vernalization of winter cereals, but the advantages to be gained, over the use of the best adapted spring varieties, would hardly justify the cost and inconvenience of preparing and planting vernalized seed. For certain genetic and breeding experiments, however, the most complete knowledge of specific environmental requirements for various stages of development is highly valuable.

According to Whyte (1948), two discoveries of importance came out of the Russian and British research on vernalization. The first is the discovery that vernalization may take place while the seed is still on the mother plant, and the second is that the process of vernalization is reversible.

Experiments by Kostjučenko and Zarubailo (1937) indicated that winter wheat of identical varieties ripened at Hibiny (lat. 67° 44′ N.) and at Kirovobad (lat. 40° 41′ N.), when planted at Hibiny the following year, showed marked differences in development. In September, following spring planting, plants from Hibiny seed had flowered and many had set seed, but plants from Kirovobad seed were at the tillering stage. This difference was said to be due to the fact that under the low temperatures at the more northern latitude the preceding autumn, partial to complete vernalization had taken place before harvest. That embryos can be vernalized on the mother plant has been definitely confirmed by Gregory and Purvis (1938a, 1938b). Whyte suggests the importance of this phenomenon in conducting variety trials using wide collections of seed and also in locating seed production areas for certain crops.

Agronomic implications of the reversibility of vernalization, according to Whyte, include the possible devernalization that might occur in mild winter areas owing to temporary periods of high temperature, after natural vernalization had been completed earlier in the winter. Also, because anaerobic conditions tend to inhibit vernalization in heavy-textured wet soils in extremely wet winters, little natural vernalization might take place.

4. Air Movement

Wind, and air movement in general, constitutes an important factor in crop distribution. Winds are caused by differences in pressure which exist as a result of temperature gradients. Wind movement is from regions of high pressure to regions of low pressure. Other than maintaining a heat balance in the atmosphere, the single most important function of wind is the transportation of water vapor from the oceans to the lands, where that water vapor condenses and falls as rain (Trewartha, 1943).

Near the Equator there is an equatorial belt of low pressure called the "doldrums," coinciding rather closely with the belt of highest temperatures. This is a region of ascending, warm moist air currents and heavy precipitation. In the region of 30° to 40° N. and S. latitude, are a series of high-pressure centers known as the "subtropical highs." These are in general regions of clear skies, subsiding air, and light precipitation. Between the doldrums and the subtropical highs are the trade-wind belts—wind blowing from the northeast in the northern hemisphere and from the southeast in the southern hemisphere. The trades bring rainfall to windward coasts of many islands and continental areas, whereas inland areas and lee coasts are likely to be arid or semiarid.

In the general region of 60° to 70° N. and S. latitude are the subpolar troughs of low pressure. Between the subtropical highs and the subpolar lows are the prevailing westerlies, which affect the climate of large areas in the middle latitudes. Borchert (1950) has suggested that the westerlies are primarily responsible for the characteristics of the climate of a large wedge-shaped area that includes much of the Great Plains region and the Prairie Peninsula, extending roughly to the lower Great Lakes region. In normal years, east of the 100th meridian, a mean tropical Atlantic (Gulf of Mexico) air flow dominates the Grassland region during the summer, and the westerlies dominate the area in winter. In years of major drought, such as 1934, the continental air flow from the west tends to displace the summer tropical Atlantic air flow from the south.

In the higher latitudes, winds blowing off the great continental glaciers become the polar easterlies. Where these winds meet the westerlies, the polar front exists, a region of clouds, storms, and precipitation. Here, irregular, changing boundaries between cold and warm air masses often result in large masses of cold air surging into middle or lower latitudes. Along this polar front many of our storms originate.

Local winds are important in determining adaptation of crops, especially in locations where land and water relationships cause regular directional breezes. Such are found along the Atlantic coast, the Great Lakes' shores, and Pacific coastal areas. Mountain and valley breezes and monsoon winds, all play an important role in influencing temperature and moisture conditions.

Superimposed over the general wind belts are migrating masses of air known as cyclones and anticyclones. Both are centers of pressure—the cyclone, low pressure, and the anticyclone, high pressure. The cyclone is usually associated with wet or cloudy weather, whereas the anticyclone is associated with dry clear weather.

A cyclone may be a region of gentle or violent winds. Hurricanes, typhoons, and tornadoes all are low-pressure centers. Hurricanes and typhoons originate near the Equator and cover a large area with violent winds and very heavy precipitation. Tornadoes, although covering much less area, are more violent. Their destructive path is usually only a few miles in length and a few hundred yards wide. In the United States tornadoes occur with greatest frequency in the Mississippi, Ohio, and lower Missouri valleys.

In mountain areas in association with cyclonic circulations, there is another wind of importance—the chinook or foehn. It is a relatively dry warm wind which descends from the mountains, warming and drying as it progresses. The chinook wind results in milder winters in the areas where it is prevalent.

Plant distribution is influenced by wind, owing to both direct mechanical effects and to indirect physiological effects. In areas of minimal moisture, protection against wind may be of great importance to crop growth. Wind may exert detrimental effects by covering plants with soil, breaking over whole plants, snapping off mature heads, shattering seed from mature plants, lacerating leaves, damaging seedlings by blowing soil, and causing loss of soil by wind erosion. Probably one of the most important effects is that of increasing transpiration and water loss in general. Other effects include dissemination of pollen and seeds, and dispersal of plant disease organisms. In the early summer, winds from the south, over the entire Mississippi valley and Great Plains area, have been most effective spreaders of rust epidemics in small grains, from early to later crop-producing areas.

5. *Climatic Analogs and Crop Adaptation*

In selecting species or varieties of crops for any region, careful attention must be given to the climatic conditions of the areas in which those crops originated.

Most of the small grain and forage crops grown in the United States were introduced from other parts of the world, and we in turn have furnished many varieties to other lands. Although it is well known that some varieties of crop plants possess a great deal of versatility, many are locally adapted, and the only way to be certain of their usefulness in a new area is to subject them to direct testing. Where wide-scale testing is not feasible, the use of climatic analogy may be helpful.

As an outgrowth of postwar problems of rehabilitation of war-devastated agricultural areas, Nuttonson (1947–1950, 1951, 1952) prepared a series of publications dealing with the agricultural climatology of a number of countries, and their agro-climatic analogs in North America. Climatic analogs are considered areas of sufficient resemblance with respect to major weather characteristics to offer a fair chance of success for plant material taken from one area to its climatic and latitudinal counterpart. For example, it was found that certain areas of Wisconsin and Minnesota are similar to areas in Czechoslovakia during the April-to-October period. Winters in Wisconsin and Minnesota, however, are more severe than in Czechoslovakia, which has a winter climate more like that of eastern Washington, eastern Oregon, and parts of Idaho. Thus both winter and summer crop analogs are important, and if in addition to the meteorological data, phenological records of several crops indicate similarity, the analogs are biologically verified.

As indicated by Nuttonson (1948), the time between date of sowing and date of flowering for a given variety may vary greatly under diverse conditions of climate and latitude. MARQUIS wheat in Alaska (64° lat.) required 78 days from sowing to heading; at Alliance, Nebraska (42° lat.), it required 97 days; and at Tlalnepantla, Mexico (19° lat.), it required 148 days. Four varieties of flax (LINOTA, REDWING, BISON, RIO) required 126 days from seeding to first bloom at Edmonton, Alberta (53° lat.), 89 days at St. Paul, Minnesota (45° lat.), and 177 days at El Centro, California (33° lat.). ALASKA peas required 63 days from planting to harvest at Matanuska, Alaska (61° lat.), 63 days at State College, Pennsylvania (41° lat.), and 75 days at College Park, Maryland (39° lat.). In all of these examples it was found that the interval between dates of sowing and flowering (or maturity) provides the least variable mathematical expression when measured in terms of a multiple of the average length of day and the summation of total days degrees (see Section IV, 2.b.3).

The possibilities of adaptation of a variety are not necessarily limited to the climatic characteristics of its place of discovery or origin. As noted by Vavilov (1951) certain species and varieties of potato (*Solanum* spp.) from the Peruvian-Bolivian region were found to produce both good tubers and seed balls beyond the Arctic Circle. Although great caution should be exercised in selecting varieties for new areas on the basis of climatic analogs, this method has been extremely helpful in supplying seed to war-devastated areas, and in nonemergency times offers promise as a means of fostering exchange of varieties for commercial production and experimental use.

6. *Vegetation as an Indication of Climate*

As noted by Billings (1952), vegetation is the product of the interaction of the environment and the genetic tolerance limits of its component species; it should therefore be a good indicator of environmental conditions. He points out, however, that it may be dangerous to predict changes in an environment because of the vegetation present. The environment occupies area independently of species. Many species have not yet occupied all of their potential environment therefore it would be incorrect to evaluate an environment on the basis of *absence* of a species. Billings states further that forests may be found in western North America in drier environments than the grasslands of the Mississippi Valley, but are maintained by a different cycle of precipitation. Beadle

(1951) has called attention to the fact that semiarid climates in New South Wales are occupied by woodlands and woody shrubs, not by grasslands as they are in the United States. In order to safely use vegetation as an indicator of environmental conditions Billings states that the vegetation must be analyzed floristically by statistical methods and that the tolerances and indicator significance of its component species must be known. Actually the vegetation is an indicator of the whole of the environment much more than of the climate alone.

V. Climate and Soil Formation

The importance of climate in the formation of soils probably was first brought to attention by Hilgard (1906) in the United States and by Dokuchaiev in Russia (see Glinka, 1935). Previously, parent material was considered the most important factor, but these workers showed that it was possible for different soils to develop from the same parent material, depending on the climate and the vegetation.

The role of climate in soil formation was discussed by Byers *et al.* (1938), the most important direct effects being the weathering of rocks and the alteration of parent material. The importance of the relative atmospheric humidity and rainfall intensity characteristics were noted. Also, the effects of high temperature in accelerating weathering and of low temperature in slowing down soil-forming processes were emphasized.

Marbut (1935) recognized the importance of climatic factors in his soil classification, starting with his first division into two groups, pedalfers and pedocals. The pedalfers, Hilgard's "humid soils," are formed in climates in which precipitation exceeds evaporation. The movement of water is predominantly downward, resulting in a marked leaching of the upper zones. The pedocals, Hilgard's "arid soils," are characterized by carbonate accumulation either at, or within a few feet of, the surface, resulting from the small downward percolation and from the upward movement of water which evaporates and deposits salts in the surface layer.

The limitations of the terms "pedalfers" and "pedocals" were pointed out by Baldwin *et al.* (1938). Some soils, such as Degraded Chernozems and Prairie soils, possess certain characteristics of both groups but do not completely fit into either category.

Jenny (1941) developed a fundamental equation of soil-forming factors

$$s = f(cl, o, r, p, t, \ldots).$$

This equation states that a soil property is dependent on the independent variables climate, organisms, relief, parent material, and time.

Although these factors may show interactions, Jenny emphasized that they also may vary independently.

To study climate, Jenny took individual climatic components, moisture and temperature, which he treated as independent factors. Two equations were set up, one expressing soil properties as functions of moisture

$$s = f(m)_{T,o,r,p,t,\ldots}$$

and the other expressing soil properties as functions of temperature

$$s = f(T)_{m,o,r,p,t,\ldots}$$

Some measure of effectiveness of rainfall, involving the relationship between precipitation and evaporation, is necessary (see Section IV, 1.b). All moisture indices have limitations in that they ignore effects of runoff, which may be of great importance, and do not take into consideration differences in capacity of various soil types to store soil moisture. Also rainfall data are only approximately correct, based on observations taken at points some distance apart and dealing only with the general macroclimate instead of the microclimate of the soil itself.

Recognizing these limitations, Jenny (1941) studied effects of moisture in relatively large areas which provided reasonable uniformity in topography, vegetation, and geologic strata, but wide variations in rainfall. In the desert and plains regions, where moisture was a limiting factor in general, as moisture increased the nitrogen and organic matter of surface soils increased. Also, with increasing moisture, clay and base saturation capacity tended to be higher, whereas concentration of soluble salts decreased. Although this relationship appeared to provide a satisfactory explanation for certain soil characteristics in the drier areas, it did not hold for the eastern forested region, where moisture was more abundant.

In considering temperature as a soil-forming factor, it should be remembered that chemical reaction rates increase exponentially with rising temperature. Weathering of rocks in the tropics proceeds at a much faster rate than in the polar regions. Jenny (1941) found that in the Mississippi Valley, within relatively uniform moisture belts containing comparable vegetation, nitrogen and organic matter in the soil decrease as the annual temperature rises. This is not to be considered a universal relationship, however, because later investigations by Jenny (1950) showed that some tropical forest soils are relatively high in nitrogen and organic matter content. No complete explanation was offered, but Jenny suggested that the predominance of legume trees, with the accompanied symbiotic fixation of nitrogen, might account for the high nitrogen content even under conditions of high average temperature.

In addition to the direct effects of climate, certain indirect effects brought about through the processes of glaciation, loess accumulation solifluction, and cryoturbation are of great importance. These processes tend to result in young or immature soils in today's cool climates (Guy D. Smith, personal communication).

Robinson (1949) has proposed a soil classification based first on differences between soils with free drainage and those with impeded drainage. This classification recognizes the importance of temperature as well as rainfall and evaporation. He points out, however, that in different parts of the world we may find examples to show that different soil-forming factors have been most important. He notes that studies in Queensland showed that in the same general climate, widely different soil types have been formed, indicating the greater importance of parent material and topography. In Russia, Robinson suggests, climatic factors have been most fruitful in classification of soils. In Great Britain he believes geology provides the best clues to soil differences. In all regions the topography, as affecting drainage and depth of accumulation of weathering products, is of great importance.

Billings (1952) has pointed out a number of instances in which parent material appears to compensate for climate. Shreve (1922) found creosote bush (*Larrea divaricata*) in Arizona growing from 900 to 1500 ft. higher on limestones than on granite. In the White Mountains of eastern California, *Pinus aristata* occurs in good stands at 11,000 ft. on dolomites, but adjacent quartzite is occupied by subalpine sagebrush-grass vegetation. In contrast, certain Sierran conifers and subalpine herbs have been found by Billings (1952) to occupy sagebrush steppe, on highly acid and infertile altered andesite sites, a considerable distance lower than their normal habitat in the Sierras.

VI. Crop Yields and the Ecological Optimum

1. *Climatic Factors and Crop Yields*

Relationships between climate and crop yields are difficult to evaluate because of the complex interactions involved. At certain growth stages, one environmental factor may be critical, whereas at other stages of development, another factor may be limiting. Correlation studies may show that yield and a certain factor of the environment vary together, but the causal effect may not be proved.

In the corn belt, the relation of climatic factors to yield was studied by Rose (1936). On the eastern edge of this region early season temperatures tended to be too low for optimum growth, whereas on the southern boundary, temperatures were too high. In the heart of the corn belt, correlations between yield and single climatic factors, such as rainfall or temperature, were extremely low. This does not mean that these factors were unimportant, but that moisture and temperature conditions approached the optimum for corn and seldom were limiting factors. Multiple correlations, involving several environmental factors and yield, usually were higher. In the moderate-to-marginal areas for corn production, the correlations between climatic factors, especially moisture, and crop yields are more likely to be significant or even critical.

Klages (1942) suggested that the Palouse area of Idaho and eastern Washington approached the ecological optimum for wheat, because consistent high yields were obtained, and the seasonal variability was low. At Pullman, Washington, where the annual precipitation is just over 20 in., the correlation between rainfall and yield of wheat was low, but at Lind 70 miles west where the annual precipitation was 8 in., the correlation was high. Another study by Klages (1934) in South Dakota indicated that the year-to-year variability in yield of wheat, oats, and barley was much greater in the central part of the state than it was at Brookings, where moisture conditions were more favorable.

Pengra (1946) reported that over a 25-year period in central South Dakota autumn and winter rainfall the preceding year was just as important as seasonal rainfall in producing small grains. With corn, seasonal rainfall was somewhat more important.

The total quantity of rainfall apparently influenced yield in more seasons than did the distribution of rainfall, as reported by Cole (1938) from studies of spring wheat production in the northern Great Plains area.

Mathews and Brown (1938) concluded from extensive studies of winter wheat yields in the southern Great Plains region that a minimum of 7.37 in. of precipitation was needed to obtain any yield; after that each 0.51 in. resulted in an average increase of 1 bu. per acre yield. In areas having but 13 in. of annual precipitation, wheat failed 80% of the time, and even with 19 to 20 in., in this region of high temperatures and erratic nature of rainfall distribution, the crop is likely to fail in one out of four years.

The effect of climatic factors on quality of crops also is of interest. Investigations by Thatcher (1913), LeClerc and Yoder (1914), Newton and Malloch (1930), and Bayfield (1936) have shown that climate exerts a marked influence on the quality of wheat and strength of flour. In marketing studies of soybeans, Pahigian (1950) reported a high degree of correlation between mean summer temperature and oil percentage. Studies by Weaver (1943a, 1943b, 1950) have shown the importance of climatic factors in barley production, particularly as they influence malting quality.

2. *Average Crop Yields and the Ecological Optimum*

A half-century ago Schimper (1903) defined the ecological optimum as a highly theoretical concept. However, if we compare average yields of crops over a wide area, a practical application of this concept is revealed. First of all it must be recognized that whereas actual crop yields are dependent on present and past production practice as well as on the natural environment, the potential yielding ability of a variety in a given area is determined largely by the combined effects of the climate and the soil. In any relatively large area, such as a county, state, or region considering farmers of all degrees of managerial ability, crop yields in the more favorable environments will be higher than those in the less favorable ones.

Long-time averages of crop yields in the Mississippi Valley, together with coefficients of variability of these yields, were presented by Klages (1930). The climate of this region varies from the typical humid woodland climate in Ohio, Indiana, and Kentucky, to the semiarid climate extending from western North Dakota south to Texas.

In this region, highest yields of corn, with lowest variability, were found in the corn belt area, centering in four states including Ohio, Indiana, Illinois, and Iowa. A gradual falling off in yield, with an increase in seasonal variability, occurred to the north, to the west, and to the south of this area. Highly fertile soils, a relatively warm and long growing season, and a rather dependable high summer rainfall were factors contributing to high yields in the corn belt.

For the production of oats, and in fact, cereal grains in general, the ecological optimum in the United States was found to be somewhat north of the corn belt. It is doubtful, however, that we have any climate as favorable to small grain production as is found in northwestern Europe. Average yields of wheat in Belgium, the Netherlands, and Denmark range close to 50 bu. per acre whereas the United States is approximately 13 bu. per acre. Small areas in Idaho, Utah, and Washington, as well as in the Delta area of Mississippi, have produced consistently high yields of cereal grains, but these are not very extensive acreages.

It would appear to be of general interest to report recent data on average yields of a few crops, in order to emphasize the importance of adaptation as well as to indicate certain marked changes which are currently taking place.

Data on corn acreage, yield per acre, and variability of yield for the 14-year period 1939 to 1952 are given in Table I. Data from states having less than 1 million acres are omitted.

TABLE I

Corn: Acreage Harvested, Yield per Acre, and Variability of Yield for Period 1939 to 1952, Inclusive

State	Acreage, thousands	Yield, bu./acre	Coefficient of variability, %
Iowa	10,335	52.0	16.3
Illinois	8,461	51.5	11.9
Ohio	3,460	49.5	12.3
Indiana	4,374	49.0	12.2
Wisconsin	2,473	43.7	11.4
Pennsylvania	1,344	42.8	9.2
Minnesota	5,168	42.5	11.1
Michigan	1,669	37.1	18.3
Missouri	4,209	34.5	19.1
Virginia	1,192	34.3	24.9
Kentucky	2,368	31.8	17.5
Nebraska	7,350	27.8	27.5
Tennessee	2,328	27 3	15.3
North Carolina	2,285	26.5	8.4
South Dakota	3,551	24.9	24.8
Kansas	2,797	23.8	26.0
North Dakota	1,161	21.2	12.4
Arkansas	1,547	19.8	22.3
Oklahoma	1,448	18.6	21.2
Mississippi	2,434	18.3	22.3
South Carolina	1,491	17.6	18.0
Louisiana	1,098	17.5	19.9
Texas	3,565	17.3	14.0
Alabama	2,930	15 8	25.5
Georgia	3,501	13.5	18.5

Yield per acre continues to be highest in the corn belt region as was shown by Klages in the long-time average. Of the total acreage in Iowa, Illinois, Indiana, and Ohio, as well as in bordering areas, nearly 100% is planted to improved hybrid varieties. Average yields in most of the southern states are low. In Texas, Rogers and Collier (1952) estimated that 65% of the total acreage was planted to hybrid corn, and it is believed that in many of the southern states the percentage may be lower than that. It is possible also that the same degree of improvement has not yet been attained in southern hybrids as has been attained in the corn belt. Losses due to insects and diseases may be greater in the South. Despite these contributing causes, probably the most important limiting factor is lack of sufficient moisture. Corn is a full-season crop and even though annual rainfall appears to be high, many areas in the southern states are subject to droughts of such regularity and intensity that yields are definitely limited. That high yields can be obtained in the South, especially on some of the more favorable soil areas, where sufficient moisture and fertilizer are available, has been adequately demonstrated.

TABLE II

Wheat: Acreage Harvested, Yield, and Variability of Yield for Period 1939 to 1952, Inclusive

State	Acreage, thousands	Yield, bu./acre	Coefficient of variability, %
	Winter Wheat		
Washington	1,756	27.8	9.6
Oregon	715	25.9	12.4
New York	342	25.7	11.2
Idaho	738	24.8	9.1
Michigan	1,003	24.3	11.4
Ohio	1,995	22.7	13.6
Pennsylvania	878	21.0	8.4
Montana	1,324	20.2	13.9
Indiana	1,441	20.2	16.7
Illinois	1,500	19.9	16.1
Utah	249	19.4	12.9
Nebraska	3,401	18.5	24.5
Colorado	1,796	18.2	24.1
Kansas	11,964	15.7	17.9
Oklahoma	5,168	13.5	21.6
	Spring Wheat (not including Durum)		
Utah	71	32.2	5.7
Idaho	418	30.7	5.4
Oregon	201	23.6	10.6
Washington	665	21.9	15.1
Colorado	145	17.5	17.6
Minnesota	1,061	17.0	13.6
Montana	3,023	15.1	22.4
North Dakota	6,981	14.3	20.6
South Dakota	2,710	11.9	24.3

The acreage of winter wheat in the United States is roughly twice that of spring wheat. In general, where both types are grown widely, winter wheat is the better crop. This probably is due to the fact that winter wheat matures earlier and can take advantage of fall and winter rains, at the same time escaping from the worst effects of summer drought. Data on wheat for the period 1939 to 1952 are given in Table II.

On a state basis, Washington would appear to be closer to the ecological optimum than any other state, with Oregon, New York, Idaho, Michigan, and Ohio all ranking fairly high. The average variability in these states is rather low as compared with that of Nebraska and Colorado, and somewhat lower than that of Kansas.

Most of the spring wheat is grown in four states, Minnesota, Montana, North Dakota, and South Dakota. Of the states with smaller acreage, Utah and Idaho rank at the top, with an extremely low year-to-year variability. Such areas approach the ecological optimum for spring wheat in the United States.

The production of alfalfa seed has developed into a rapidly changing and interesting pattern. Data on production of this crop are presented in Table III.

TABLE III

Alfalfa Seed: Acreage Harvested, Yield, and Variability of Yield for Period 1943 to 1952, Inclusive

State	Acreage for seed	Yield, lb./acre	Coefficient of variability, %
Washington	9,470	309	68.5
California	46,700	265	32.2
Arizona	44,100	187	26.7
Texas	16,100	177	20.2
Utah	46,000	148	36.6
Idaho	28,900	136	24.5
Colorado	22,500	110	17.1
Oklahoma	95,000	107	12.2
Montana	80,800	85	19.9
Kansas	152,700	82	17.6
Nebraska	106,500	67	17.7
Wisconsin	19,900	62	32.4
Minnesota	49,500	55	18.0
South Dakota	55,600	55	27.5
Michigan	47,400	47	18.7
North Dakota	40,900	46	22.4
Iowa	8,010	45	18.5

Average yields per acre for the period 1943 to 1952 show a rather gradual but definite increase from east to west, in sharp contrast to yields of corn. Data for the western states, particularly Washington and California, do not adequately show the present picture because both the acreage and yield per acre have increased sharply during the last five years. The acreage currently grown is more than twice that reported for both states, and the yields per acre also are much higher.

Low yields in the Midwest are due to high summer rainfall, lack of dry, bright weather during flowering season, excessive insect and disease damage to foliage, buds, flowers, and pods, and lack of sufficient pollinating insects. Under the more favorable climatic conditions in the West, with irrigation for moisture control, adequate spray programs for insect control, greater populations of pollinators and better harvesting methods, seed yields have increased greatly. These rapid changes in acreages and production practices result in high variability, but on a five-year basis this variability would be considerably lower. It is only since 1947 that present practices have been in extensive use. In 1946 the average yield of alfalfa seed per acre in Washington was 150 lb.; in 1950 it was 540 lb. Wallace (1920) and Fisher (1921) noted that trends in long-time yields must be given consideration, and sharp deviations may upset what otherwise appear to be stable relationships.

One of the greatest weaknesses in the use of the data presented is the use of state averages. States vary greatly in size, topography, and location, and state lines are not likely to represent ecological divisions. Two suggestions might be made to improve such studies. The first is that more extensive, and at the same time more accurate, meteorological observations are needed, including data on the plant climate or microclimate. The second suggestion is that yield data should be accumulated on an ecological unit basis rather than a state basis. Although this may not be possible directly, data on a county basis would be a step in the right direction. Then counties with similar climatic and soil conditions could be grouped into larger units for studies of variability and of climate-yield relationships.

REFERENCES

Åkerberg, Erik. 1948. "Svalof 1886–1946." Carl Bloms, Lund, Sweden.

Allard, H. A., and Evans, M. W. 1941. *J. Agr. Research* **62**, 193–228.

Allard, H. A., and Garner, W. W. 1940. *U. S. Dept. Agr. Tech. Bull.* **727.**

Allee, W. C., and Park, Thomas. 1939. *Science* **89**, 166–169.

Andrews, J., and Maze, W. H. 1933. *Proc. Linnean Soc. N. S. Wales* **58**, 105.

Baldwin, Mark, Kellogg, C. E., and Thorp, J. 1938. U. S. Dept. Agr. Yearbook, pp. 979–1001.

Barger, G. L., and Thom, H. C. S. 1949a. *Agron. J.* **41**, 13–19.

Barger, G. L., and Thom, H. C. S. 1949b. *Agron. J.* **41**, 519–526.

Barnard, J. 1948. *Canner* **106**, 28.

Bayfield, E. G. 1936. *Ohio Agr. Expt. Sta. Bull.* **563.**

Beadle, N. C. W. 1951. *Ecology* **32,** 343–345.

Billings, W. D. 1952. *Quart. Rev. Biol.* **27,** 251–265.

Blackman, F. F. 1905. *Ann. Botany* (London) **19,** 281–295.

Bomalaski, H. H. 1948. *Food Packer* **29,** 51; *ibid.* **29,** 57.

Bonner, J. 1944. *Botan. Gaz.* **105,** 233–243.

Bonnett, O. T. 1936. *J. Agr. Research* **53,** 445–451.

Borchert, J. R. 1950. *Ann. Assoc. Am. Geog.* **40,** 1–39.

Borthwick, H. A., Hendricks, S. B., and Parker, M. W. 1948. *Botan. Gaz.* **110,** 103–118.

Borthwick, H. A., Parker, M. W., and Hendricks, S. B. 1950. *Am. Naturalist* **84,** 117–134.

Borthwick, H. A., Hendricks, S. B., Parker, M. W., Toole, E. H., and Toole, V. K. 1952. *Proc. Natl. Acad. Sci. U. S.* **38,** 662–666.

Borthwick, H. A., Hendricks, S. B., Parker, M. W., Toole, E. H., and Toole, V. K. 1953. *Agr. Research* **1** (No. 3), 3–5.

Briggs, L. J., and Shantz, H. L. 1912a. *U. S. Dept. Agr. Bur. Plant Industry Bull.* **230.**

Briggs, L. J., and Shantz, H. L. 1912b. *Botan. Gaz.* **53,** 229–235.

Briggs, L. J., and Shantz, H. L. 1913. *U. S. Dept. Agr. Bur. Plant Industry Bull.* **284.**

Briggs, L. J., and Shantz, H. L. 1914. *J. Agr. Research* **3,** 1–64.

Brooks, C. F. 1935. "Why the Weather?" Harcourt, Brace & Company, New York.

Byers, H. R. 1937. "Synoptic and Aeronautical Meteorology." McGraw-Hill Book Co., New York.

Byers, H. G., Kellogg, C. E., Anderson, M. S., and Thorp, James. 1938. U. S. Dept. Agr. Yearbook, pp. 948–978.

Cain, S. A. 1944. "Foundations of Plant Geography." Harper and Brothers, New York.

Camp, W. B. 1949. *Better Crops with Plant Food* **33,** 9–12, 47.

Clausen, J. 1949. *Proc. 8th Intern. Congr. Genet.*, pp. 162–172.

Clausen, J. 1951. "Stages in the Evolution of Plant Species." Cornell University Press, Ithaca, New York.

Clausen, J., Keck, D. D., and Hiesey, W. M. 1940. *Carnegie Inst. Wash. Publ.* **520.**

Clausen, J., Keck, D. D., and Hiesey, W. M. 1941. *Am. Naturalist* **75,** 231–250.

Clausen, J., Keck, D. D., and Hiesey, W. M. 1945. *Carnegie Inst. Wash. Publ.* **564.**

Clausen, J., Keck, D. D., and Hiesey, W. M. 1947. *Am. Naturalist* **81,** 114–133.

Clements, H. F. 1940. *Hawaiian Planters' Record* **44,** 201–233.

Clements, H. F. 1951. "Mineral Nutrition of Plants," pp. 451–469. University of Wisconsin Press, Madison, Wisconsin.

Cole, J. S. 1938. *U. S. Dept. Agr. Tech. Bull.* **636.**

Curtis, O. F. 1936. *Plant Physiol.* **11,** 343–364.

Darwin, C. 1872. "Origin of Species, by Means of Natural Selection." John Murray, London.

Daubenmire, R. F. 1947. "Plants and Environment." John Wiley & Sons, New York.

Davis, D. H. 1948. "Earth and Man." The Macmillan Co., New York.

Decker, A. M. 1953. Ph. D. Thesis. University of Maryland, College Park, Maryland.

De Martonne, E. 1926. *Compt. rend.* **182,** 1395–1398.

Dobzhansky, T. 1950. *Science* **111,** 161–166.

Dobzhansky, T. 1951. "Genetics and the Origin of Species." Columbia University Press, New York.

Evans, M. W. 1931. *Ecology* **12,** 182–187.

Evans, M. W., and Allard, H. A. 1934. *J. Agr. Research* **48**, 571–586.

Evans, M. W., Allard, H. A., and McConkey, O. 1935. *Sci. Agr.* **15**, 573–579.

Evans, M. W., and Grover, F. O. 1940. *J. Agr. Research* **61**, 481–520.

Evans, M., and Wilsie, C. P. 1946. *J. Am. Soc. Agron.* **38**, 923–932.

Fisher, R. A. 1921. *Trans. Royal Soc. (London)* **B213**, 89–142.

Foster, E. E. 1948. "Rainfall and Runoff." The Macmillan Company, New York.

Gardner, F. P., and Loomis, W. E. 1953. *Plant Physiol.* **28**, 201–217.

Garner, W. W. 1933. *Plant Physiol.* **8**, 347–356.

Garner, W. W. 1937. *Botan. Rev.* **3**, 259–275.

Garner, W. W., and Allard, H. A. 1920. *J. Agr. Research* **18**, 553–605.

Garner, W. W., and Allard, H. A. 1923. *J. Agr. Research* **23**, 871–920.

Garner, W. W., and Allard, H. A. 1930. *J. Agr. Research* **41**, 719–735.

Garner, W. W., and Allard, H. A. 1931. *J. Agr. Research* **43**, 439–443.

Gassner, G. 1918. *Z. Botan.* **10**, 417–430.

Geiger, R. 1950. "Climate Near the Ground." Harvard University Press, Cambridge.

Glinka, K. D. 1935. "Great Soil Groups of the World and Their Development," Trans. from German by C. F. Marbut. Edwards Bros., Ann Arbor, Mich.

Good, R. 1931. *New Phytologist* **30**, 149–171.

Good, R. 1953. "Geography of the Flowering Plants." Longmans, Green & Company, London.

Gregor, J. W. 1931. *New Phytologist* **30**, 204–217.

Gregor, J. W. 1944. *Biol. Revs. Cambridge Phil. Soc.* **19**, 20–30.

Gregor, J. W. 1946. *New Phytologist* **45**, 254–270.

Gregor, J. W., Davey, V., and Lang, J. 1936. *New Phytologist* **35**, 323–350.

Gregor, J. W., and Sansome, F. W. 1930. *J. Genet.* **22**, 373–387.

Gregory, F. G., and Purvis, O. N. 1938a. *Ann. Botany (London)* **2**, 237–251.

Gregory, F. G., and Purvis, O. N. 1938b. *Ann. Botany (London)* **2**, 753–764.

Hamner, K. C. 1944. *Ann. Rev. Biochem.* **13**, 575–590.

Hamner, K. C., and Bonner, J. 1938. *Botan. Gaz.* **100**, 388–431.

Hanson, A. A., and Sprague, V. G. 1953. *Agron. J.* **45**, 248–251.

Harlan, H. V., and Martini, M. L. 1938. *J. Agr. Research* **57**, 189–200.

Harlan, Jack R. 1951. *Am. Naturalist* **85**, 97–103.

Hendricks, S. B., and Borthwick, H. A. 1953. *Agr. Research* **2** (No. 1), 14.

Hilgard, E. W. 1906. "Soils." The Macmillan Company, New York.

Holt, Imy V. 1952. M. S. Thesis. Iowa State College, Ames, Iowa.

Hoover, W. H. 1937. *Smithsonian Misc. Collections* **95**.

Hoover, W. H., Johnson, E. S., and Brackett, F. S. 1933. *Smithsonian Misc. Collections* **87** (16).

Hopkins, A. D. 1938. *U. S. Dept. Agr. Misc. Publ.* **280**.

Humphreys, W. J. 1941. "Physics of the Air." McGraw-Hill Book Co., New York.

Huxley, Julian. 1950. *World Review (London)* Jan., 7–14.

Jacobs, W. P. 1951. *Science* **116**, 205–206.

Jenny, Hans. 1941. "Factors of Soil Formation." McGraw-Hill Book Company, New York.

Jenny, Hans. 1950. *Soil Sci.* **69**, 63–69.

Katz, Yale H. 1952. *Agron. J.* **44**, 74–78.

Kemp, W. B. 1937. *J. Heredity* **28**, 329–333.

Kendrew, W. G. 1942. "The Climates of the Continents." Oxford University Press, Oxford.

Kiesselbach, T. A. 1915. *Nebraska Agr. Expt. Sta. Research Bull.* **6**.

Kiesselbach, T. A. 1950. *Nebraska Agr. Expt. Sta. Research Bull.* **166.**

Kiesselbach, T. A., Anderson, A., and Russel, J. C. 1934. *J. Am. Soc. Agron.* **26,** 422–442.

Kiesselbach, T. A., Russel, J. C., and Anderson, A. 1929. *J. Am. Soc. Agron.* **21,** 241–268.

Kincer, J. B. 1941. U. S. Dept. Agr. Yearbook, pp. 685–699.

Klages, H. K. W. 1926. *J. Am. Soc. Agron.* **18,** 529-566.

Klages, H. K. W. 1930. *Ecology* **11,** 293–306.

Klages, H. K. W. 1934. *Ecology* **12,** 334–345.

Klages, H. K. W. 1936. *J. Am. Soc. Agron.* **28,** 935-940.

Klages, H. K. W. 1942. "Ecological Crop Geography." The Macmillan Book Company, New York.

Klebs, G. 1918. *Flora* (Ger.) **111–112,** 128–151.

Klippart, John H. 1858. *Ann. Rept. Ohio State Board Agr.*, p. 757.

Knight, W. E., and Bennett, Hugh. 1953. *Agron. J.* **45,** 268–269.

Knott, J. E. 1932. *Proc. Am. Soc. Hort. Sci.* **31,** 152–154.

Knowles, R. P., and White, W. J. 1949. *Sci. Agr.* **29,** 437–450.

Köppen, W. 1931. "Grundriss der Klimakunde." Walter de Gruyter, Berlin.

Kostjučenko, I. A., and Zarubailo, T. 1937. *Herbage Revs.* **5,** 146–157.

Lana, E. P., and Haber, E. S. 1951. *Iowa State Coll. J. Sci.* **26,** 99–109.

Laude, H. H., and Swanson, A. F. 1942. *J. Am. Soc. Agron.* **34,** 270–274.

LeClerc, J. A., and Yoder, P. A. 1914. *J. Agr. Research* **6,** 275–291.

Lehenbauer, P. A. 1914. *Physiol. Researches.* **1,** 247–288.

Leopold, A. C. 1951. *Quart. Rev. Biol.* **26,** 247–263.

Liebig, J. 1862. "Die Chemie in ihrer Anwendung auf Agricultur und Physiologie," 7e Aufl, Vol. 2. F. Vieweg und Sohn, Braunschweig.

Livingston, B. E. 1916. *Physiol. Researches* **1,** 421–440.

Livingston, B. E., and Livingston, Grace J. 1913. *Botan. Gaz.* **56,** 349–375.

Ludwig, R. A., Barrales, H. G., and Steppler, H. 1953. *Can. J. Agr. Sci.* **33,** 274–287.

McKinney, H. H., and Sando, W. J. 1933. *J. Heredity* **24,** 169–179.

Major, Jack, 1951. *Ecology* **32,** 392–412.

Mangelsdorf, Paul. 1952. *Am. Naturalist* **86,** 65–77.

Marbut, C. F. 1935. "Atlas of American Agriculture." Part 3. "Soils of the United States." Government Printing Office, Washington, D. C.

Mason, H. L. 1936. *Madroña* **3,** 181–190.

Mathews, O. R., and Brown, L. A. 1938. *U. S. Dept. Agr. Circ.* **477.**

Metcalfe, D. S. 1950. Ph D. Thesis, Iowa State College, Ames, Iowa.

Meyer, A. 1926. *Chemie der Erde* **2,** 209–347.

Meyer, B. S., and Anderson, D. B. 1952. "Plant Physiology." D. Van Nostrand Company, New York.

Murneek, A. E., and Whyte, R. O. 1948. "Vernalization and Photoperiodism." Chronica Botanica, Waltham, Massachusetts.

Myers, H. E. 1936. *J. Am. Soc. Agron.* **28,** 106–114.

Naylor, F. L. 1941. *Botan. Gaz.* **103,** 146–154.

Nettles, V. F., Jamison, F. S., and Janes, B. E. 1952. *Florida Agr. Expt. Sta. Bull.* **495.**

Newton, R., Malloch, J. G. 1930. *Sci. Agr.* **10,** 669–677.

Noguchi, Y. 1929. *J. Coll. Agr. Tokyo Imp. Univ.* **10,** 247–304.

Nuttonson, M. Y. 1947–1950. *Am. Inst. Crop Ecology Intern. Agro-Climat. Series* **1–13.** Washington, D. C.

Nuttonson, M. Y. 1948. In "Vernalization and Photoperiodism" (Murneek and Whyte eds.). Chronica Botanica, Waltham, Mass., 129–143.

Nuttonson, M. Y. 1951. "Ecological Crop Geography and Field Practices in Japan." American Institute of Crop Ecology, Washington, D. C.

Nuttonson, M. Y. 1952. "Ecological Crop Geography and Field Practices of the Ryukyus." American Institute of Crop Ecology, Washington, D. C.

Olmsted, C. E. 1943. *Botan. Gaz.* **105,** 165–187.

Olmsted, C. E. 1944. *Botan. Gaz.* **106,** 46–74.

Olmsted, C. E. 1945. *Botan. Gaz.* **107,** 382–401.

Pahigian, N. 1950. *Soybean Marketing Studies P. M. A. Fats and Oils Branch, U. S. Dept. Agr.*, Sept.

Palmer, A. E. 1949. *Progress Report 1937–1946. Dominion Expt. Sta., Lethbridge, Alberta.*

Parks, R. Q. 1951. *Advances in Agron.* **3,** 323–344.

Pearson, G. A. 1924. *Monthly Weather Rev.* **52,** 218–220.

Pearson, G. A. 1931. *U. S. Dept. Agr. Tech. Bull.* **247.**

Penck, A. 1910. *Sitz. ber. Preuss. Akad. Wiss. Physik-math. Kl.*, pp. 236–246.

Pengra, R. F. 1946. *J. Am. Soc. Agron.* **38,** 848–850.

Perrin, H. 1931. *Compt. rend.* **192,** 1271.

Peterson, M. L., and Loomis, W. E. 1949. *Plant Physiol.* **24,** 31–43.

Petterssen, S. 1941. "Introduction to Meteorology." McGraw-Hill Book Company, New York.

Pfeffer, W. 1903. "Physiology of Plants," Vol. 2, trans. by A. J. Ewart, Clarendon Press, Oxford.

Pfeiffer, Norma E. 1928. *Botan. Gaz.* **85,** 427–436.

Phillips, E. E. 1950. *Canner* **110,** 10–24.

Pritchett, W. L., and Nelson, L. B. 1951. *Agron. J.* **43,** 172–177.

Purvis, O. N. 1934. *Ann. Botany (London)* **48,** 919–955.

Purvis, O. N. 1940. *Nature* **145,** 462.

Purvis, O. N. 1944. *Ann Botany (London)* **8,** 285–314.

Purvis, O. N., and Gregory, F. G. 1937. *Ann. Botany (London)* **1,** 569–591.

Purvis, O. N., and Gregory, F. G. 1945. *Nature* **155,** 113–114.

Richardson, A. E. V., and Trumble, H. C. 1928. *J. Agr. S. Australia* **32,** 224–244.

Roberts, R. H., and Struckmeyer, B. E. 1939. *J. Agr. Research* **59,** 699–709.

Robinson, Gilbert W. 1949. "Soils, Their Origin, Constitution and Classification." Thomas Murby and Co., London.

Rogers, John S., and Collier, J. W. 1952. *Texas Agr. Expt. Sta. Bull.* **746.**

Rose, J. K. 1936. *Geog. Rev.* **26,** 88–102.

Sanderson, Marie. 1950. *Can. J. Research,* **C28,** 482–492.

Sass, John E., and Skogman, Jane. 1951. *Iowa State Coll. J. Sci.* **25,** 513–519.

Schimper, A. F. W. 1903. "Plant Geography on a Physiological Basis." Clarendon Press, Oxford.

Sellschop, J. P. F., and Salmon, S. C. 1928. *J. Agr. Research* **37,** 315–338.

Shantz, H. L., and Piemeisel, L. N. 1927. *J. Agr. Research* **34,** 1093–1190.

Sharman, B. C. 1942. *Nature* **149,** 82.

Sharman, B. C. 1945. *Botan. Gaz.* **106,** 269–289.

Shaw, R. H., Barger, G. L., and Thom, H. C. S. 1954. *Special Report Series Iowa State College.* **No. 6.**

Shaw, Byron, 1953. *Agron. J.* **45,** 85–92.

Shirley, H. L. 1929. *Am. J. Botany* **16,** 354–390.

Shirley, H. L. 1945. *Botan. Rev.* **11**, 497–532.

Shreve, Forrest. 1922. *Ecology* **3**, 269–274.

Simonovitch, D., and Scarth, G. W. 1938. *Can. J. Research* **C16**, 467–481.

Snyder, W. E. 1940. *Botan. Gaz.* **102**, 302–322.

Stamp, L. Dudley. 1952. "Land for Tomorrow." Indiana University Press, Bloomington, Indiana.

Stapledon, R. G. 1928. *J. Ecol.* **16**, 71–104.

Stebbins, G. L., Jr. 1950. "Variation and Evolution in Plants." Columbia University Press, New York.

Stuckey, Irene H., and Curtis O. F. 1938. *Plant Physiol.* **13**, 815–833.

Suneson, C. A., and Wiebe, G. A. 1942. *J. Am. Soc. Agron.* **34**, 1052–1056.

Sylven, N. 1937. *Imperial Bur. Plant Genetics Herbage Plants Bull.* **21**.

Szymiekwicz, D. 1925. *Acta. Soc. Botan. Polon.* **2**, 239–253.

Taylor, Walter P. 1934. *Ecology* **15**, 374–379.

Thatcher, R. W. 1913. *Washington Agr. Expt. Sta. Bull.* **111**.

Thomas, R. O. 1948. *Iowa State Coll. J. Sci.* **23**, 86–88.

Thorne, D. W., and Peterson, H. B. 1949. "Irrigated Soils, Their Fertility and Management." Blakiston Company, Philadelphia.

Thornthwaite, C. W. 1931. *Geog. Rev.* **21**, 633–655.

Thornthwaite, C. W. 1933. *Geog. Rev.* **23**, 433–440.

Thornthwaite, C. W. 1943. *Geog. Rev.* **33**, 233–255.

Thornthwaite, C. W. 1948. *Geog. Rev.* **38**, 55–94.

Thornthwaite, C. W. 1951. *Bull. Am. Meteorol. Soc.* **32**, 166–173.

Transeau, E. N. 1905. *Am. Naturalist* **39**, 875–889.

Trewartha, G. T. 1943. "An Introduction to Weather and Climate." McGraw-Hill Book Company, New York.

Trumble, H. C. 1937. *Trans. Roy. Soc. S. Australia* **61**, 41–62.

Trumble, H. C. 1939. *Trans. Roy. Soc. S. Australia* **63**, 36–43.

Turesson, G. 1922a. *Hereditas* **3**, 100–113.

Turesson, G. 1922b. *Hereditas* **3**, 211–350.

Turesson, G. 1927. *Hereditas* **9**, 81–101.

Turesson, G. 1930. *Hereditas* **14**, 99–152.

Turrill, W. B. 1940. "Experimental and Synthetic Taxonomy." *In* "The New Systematics," (J. Huxley, ed.), pp. 47–71. Clarendon Press, Oxford.

Turrill, W. B. 1946. *New Phytologist* **45**, 34–43.

van Bavel, C. H. M. 1953. *Agron. J.* **45**, 167–172.

Vavilov, N. I. 1922. *J. Genetics* **12**, 47–89.

Vavilov, N. I. 1926. "Studies in the Origin of Cultivated Plants." Inst. Appl. Botany and Plant Breed., Leningrad.

Vavilov, N. I. 1951. "The Origin, Variation, Immunity and Breeding of Cultivated Plants," trans. from Russian by K. Starr Chester. Chronica Botanica, Waltham, Massachusetts.

Veihmeyer, F. J. 1938. *Trans Am. Geophys. Union,* **19**, 612–619.

Veihmeyer, F. J., and Hendrickson, A. H. 1948. *Soil Sci.* **65**, 487–493.

Veihmeyer, F. J., and Hendrickson, A. H. 1950. *Ann. Rev. Plant Physiol.* **1**, 285–304.

Vogt, Wm. 1948. "The Road to Survival." W. Sloane Assoc., New York.

Voss, J. 1938. *Pflanzenbau* **15**, 1–35, 49–79.

Waggoner, P. E., and Shaw R. H. 1952. *Plant Physiol.* **27**, 710–724.

Wallace, Henry A. 1920. *Monthly Weather Rev.* **48**, 439–446.

Weaver, John C. 1943a. *Geog. Rev.* **33,** 56–73.
Weaver, John C. 1943b. *Geog. Rev.* **33,** 569–588.
Weaver, John C. 1950. "American Barley Production." Burgess, Minneapolis.
Went, F. W. 1944. *Am. J. Botany* **1,** 135–150.
Went, F. W. 1945. *Am. J. Botany* **32,** 469–479.
Went, F. W. 1948. *In* "Vernalization and Photoperiodism" (Murneek and Whyte eds.), pp. 145–157. Chronica Botanica, Waltham, Massachusetts.
Went, F. W. 1950. *Science* **112,** 489–494.
Whyte, R. O. 1946. "Crop Production and Environment." Faber and Faber, London.
Whyte, R. O. 1948. "Vernalization and Photoperiodism," pp. 1–38. Chronica Botanica, Waltham, Massachusetts.
Widtsoe, J. A. 1909. *Utah Agr. Expt. Sta. Bull.* **105.**
Wiggans, S. C. 1953. *Proc. Iowa Acad. Sci.* **60,** 278–284.

Potassium in Plant Nutrition

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I. INTRODUCTION

The importance of potassium in crop production has been recognized only since the beginning of the nineteenth century, although the benefits of organic or inorganic materials containing potassium were recognized many years earlier. Animal manures, dried plant residues, and wood ashes have long been considered as valuable amendments for agricultural soils. As interest in the effects of salts on plant growth increased, knowledge of the relationship of potassium to plant growth accumulated rapidly. Work by Boussingault, Sprengel, Liebig, and Lawes and Gilbert led to the appreciation of the place of potassium in plant nutrition. Thereafter, studies of potassium in soils and plants were conducted by those associated with agronomy, plant physiology, horticulture, and geology. A voluminous amount of research has been conducted in each of these fields, and remarkable advances have been made. However, as is true in all sciences, the very search for solutions to problems brings forth new and unanswered questions and relationships.

II. ROLE OF POTASSIUM IN PLANT GROWTH

As an essential element for plant growth, potassium presents a challenge to workers who wish to establish its role and exact functions in plants. Unlike nitrogen, phosphorus, calcium, and magnesium, the potassium ion does not enter into permanent organic combinations in plants, but apparently exists as soluble inorganic and organic salts.

Consequently it is difficult to assign specific roles within closely related physiological processes. Researches over the years have shown that potassium is essential for various metabolic activities of living cells. A lack of sufficient potassium for normal growth causes disturbances in one or more vital plant processes resulting in the appearance of visual symptoms of disorder. By comparing certain constituents and properties of plants starved for potassium with those of normal plants, much insight has been gained regarding the influence of this element on the physiology of plants. This subject has been ably reviewed by Miller (1938), Hoffer (1938), Nightingale (1943), and Steinberg (1951).

Evidence is now available which shows that potassium affects the following processes: (1) synthesis of simple sugars and starch, (2) translocation of carbohydrates, (3) reduction of nitrates and synthesis of proteins, particularly in meristem tissues, and (4) normal cell division. In addition it has been suggested that potassium may play a part in the maintenance of turgor in plant cells as well as in the formation of oils and in the enhancement of disease resistance. A few investigators have postulated that potassium affects photosynthesis and other physiological processes indirectly through its influence on chlorophyll components or by radiation from naturally occurring radioactive isotopes.

1. Carbohydrate Accumulation

It is generally recognized that directly or indirectly potassium is an important factor in carbon dioxide assimilation in plants. Early studies by Hellriegel (1898) and Wilfarth and Wimmer (1902) demonstrated a close relationship between carbohydrates and potassium level. More recent experiments by Gregory (1937), Shive and Robbins (1939), Sommers (1941), and others have lent further credence to this relationship. Nightingale (1942) has clearly shown that pineapple plants well supplied with potassium contained significantly more carbohydrates than did plants deficient in this element. Wall (1940) also noted an ultimate decrease in carbohydrates when potassium was withheld from tomato plants in solution culture. In addition Gregory and Sen (1937) reported decreased carbon dioxide assimilation and increased respiration in potassium-deficient barley plants.

These data are not in agreement with work by Lundegardh (1932), who reported no reduction in photosynthetic activity by oats grown in potassium-deficient sand culture. Hibbard and Grigsby (1934) found that garden peas growing in minus potassium solutions produced simple sugars, sucrose, starch, hemicellulose, and proteins, but in less quantity than plants grown in complete nutrient solution. They concluded that a lack of potassium retarded protoplasmic mechanisms, which in turn retarded carbohydrate accumulation and other processes.

Although a decrease in carbohydrates is associated with severe potassium deficiency, a number of workers including Nightingale *et al.* (1930), Turtschin (1934), Hartt (1934), and Wall (1939) have reported an initial accumulation of carbohydrates in potassium-deficient plants. On the other hand, Gregory (1937) noted no such apparent accumulation in the early stages of potassium starvation. Investigations by Wall (1940) have indicated that nitrogen metabolism is affected prior to carbohydrate metabolism. If this is true, the initial accumulation of carbohydrates is probably the result of a lack of utilization of soluble organic nitrogen.

Considerable interest has been centered around the relative proportion of reducing sugars to total carbohydrates in potassium-deficient and normal plants. A recent study of the nitrogen and potassium levels in Tung seedlings by Loustalot *et al.* (1950) revealed there was an increase in reducing sugars and a decrease in nonreducing sugars, especially in roots, when available soil potassium was low. They suggested that potassium might play a role in condensing hexose to disaccharide sugars, providing sucrose is not considered to be the primary product of photosynthesis. Steinberg (1951) has listed the deficiency control ratios for reducing sugars and carbohydrates of ten crop plants as reported by various investigators. In general, a lack of potassium led to an accumulation of reducing sugar compared to total carbohydrate. However, he emphasized that the extent and duration of deficiencies might result in variable proportions of carbohydrates and reducing sugars.

One plant characteristic which has been widely studied with respect to the influence of potassium is the structure of stems and cell walls. The general belief from observation and experiments is that stiffness of straw or stalk is related to an adequate supply of potassium within the plant. Nightingale (1943) pointed out that when carbohydrates are abundant, stem structures are likely to be strongest. Certainly the development of lignin and cellulose will be limited in cases of low carbohydrate accumulation. However, if carbohydrates are utilized in protein synthesis as fast as they are produced, as when nitrate supplies are high, cell walls may be thin and stems weak even though the plant tissues contain adequate levels of potassium.

Recently Boyer *et al.* (1943) found that in muscle tissue potassium ions accelerated the reaction involving the transfer of the phosphate group of 2-phosphopyruvate to the adenylic system, thus making energy available for biological processes. In this sense potassium acts as an enzyme activator, and it is probable this specific action also takes place in plants.

2. *Nitrate Absorption*

Nightingale (1943) and others have suggested that the uptake of the nitrate ion by plants is greatly accelerated by the presence of cations such as potassium and calcium. This relationship apparently does not hold for all species of plants and may be complicated by other factors controlling nitrate absorption. For certain crops such as pineapples and some tree fruits, potash fertilizer is being used to control carbohydrate–nitrogen relationships. When carbohydrates are high and nitrates are needed for protein synthesis, additional potassium is required by the plant. This practice is especially important when an excess of nitrates might cause extensive and undesirable vegetative growth.

3. *Nitrate Reduction and Protein Synthesis*

Many investigators have suggested that potassium has a marked influence on the reduction of nitrates and synthesis of proteins in plants. The conclusion of some workers is that the effect is a direct one, although Richards and Templeman (1936), Gregory (1937), and others feel that potassium exerts an indirect influence on nitrogen metabolism. It is generally agreed, however, that relative to normal plants potassium-deficient plants are high in soluble organic nitrogen fractions such as amino and amide forms, though whether these nitrogen fractions are of a synthesized or degraded nature is open to question. In eight out of nine investigations, Steinberg (1951) reports that deficiency/control ratios were higher for amino acid nitrogen than for protein nitrogen. Nightingale *et al.* (1930) were able to demonstrate increased nitrate reduction when potassium-deficient tomato plants were placed in a solution of potash salts. Potassium ions were quickly absorbed and for a short time a very high concentration of nitrite was evident in the plant tissues.

The hypothesis involving potassium in a direct relationship to nitrogen metabolism suggests that the organic nitrogen fractions are increased as a result of a disturbance in protein synthesis. On this basis Hartt (1943), Wall (1940), and others have accounted for the initial accumulation of carbohydrates in the early stages of potassium starvation. Those investigators supporting the opposite view consider the high levels of soluble organic nitrogen to be a result of a breakdown of proteins. However, Wall (1940) has pointed out that proteolysis does not occur at a high rate if abundant carbohydrates are present.

His data show that the increases in ammonia, amide, and amino nitrogen were correlated with initial accumulation of carbohydrates, indicating that protein synthesis was interrupted. It has been demonstrated that when plants are grown in solutions high in ammonia and low in potassium, the tissues may die from ammonium toxicity because of the retardation of protein synthesis.

4. Cell Division

Data by Nightingale *et al.* (1930) and James and Penston (1933) emphasize the fact that high potassium concentrations are associated with actively growing plant tissues. When soil potassium is insufficient for maximum growth, it is commonly transported from mature to meristematic regions. The older leaves may then exhibit deficiency symptoms and die as a result.

Most cytological studies have shown that potassium seems to be absent from the nucleus and chloroplasts of plant cells. It has been reported in both cytoplasm and vacuoles. A lack of agreement as to its location in the cell may be due to variations in plant species and in the kind and maturity of cells studied. The function of potassium in cell division is not clear, although it is probably connected with the synthesis of proteins.

Using a special precipitation technique involving a freezing microtome, Dowding (1925) was able to study the distribution of potassium in various plant tissues. He noted its absence from the wood of mature roots of the spruce (*Picea canadensis*), but meristematic cells were especially high in this element. When the spruce bud elongated there was translocation of the potassium within the embryonic cone to next year's meristem and embryonic leaves. In summer the potassium in the mesophyll occurred as a network of granules between the chloroplasts. The fine rootlets contained much more potassium than did older roots, with the tracheids being unusually rich, whereas very little was noted in the cortex tissue.

5. Formation of Organic Acids and Oils

Recent data by Vladimirov (1945) established the fact that the effect of potassium on the metabolism of organic acids depends upon the form of nitrogen in the growing medium. In plants treated with nitrate nitrogen, an increase in potassium caused a decrease in content of organic acid, whereas in plants receiving ammonia nitrogen, there was an increase in organic acid. In the first situation potassium probably stimulated reduction processes, but in the presence of ammonia nitrogen, it promoted oxidation processes in the plants.

A number of investigations have shown that fertilizer potassium increased the oil content of certain crops. Nelson *et al.* (1945) reported that liberal applications of potash fertilizer to a soil low in potassium increased the oil content of two varieties of soybeans an average of 1.5 per cent. Drosdoff *et al.* (1947) noted that on a potassium-deficient soil, fruit from tung trees treated with potash fertilizer was higher in oil and lower in sucrose than fruit from deficient trees. On this basis they suggested that potassium helps in the transformation of sugar to oil. Brown and Potter (1949) also reported significant increases in yield and oil content of fruit from tung trees fertilized with potassium. In studies with bay trees in Puerto Rico, Loustalot (1949) found that potash fertilizers had no appreciable effect on yield of oil.

6. Resistance to Disease

It has been reported that potassium is influential in increasing the resistance of certain crops to specific diseases. Whether potassium enables the plant to withstand attacks of organisms or whether the organisms become established more easily in potassium-deficient tissues than in normal tissues is not known.

Some workers have noted a relationship between the incidence of bacterial leaf spot and the potassium supply available to the tobacco plant. According to Haley and Reid (1943) the role of this element in disease is not well understood, but they believe that potassium deficiency is associated with a susceptibility to leaf spotting. Disease resistance accompanied high quality, and such tobacco contained at least as much potassium as nitrogen. However, all fields heavily fertilized with potassium did not produce high-quality disease-resistant plants.

The control of cotton wilt by the use of suitable varieties together with the use of fertilizers containing adequate amounts of potash has been suggested by a number of investigators. Studies on cotton wilt by Tisdale and Dick (1942) showed that varieties differ with respect to potassium requirements for normal development and for withstanding wilt attacks. At two locations in Alabama, heavy applications of potassium were very beneficial to susceptible varieties when wilt was not severe. At another location, only the resistant varieties responded to potash fertilizer when the wilt was especially severe.

It has been pointed out by Hoffer (1949) that when potassium deficiency occurs in corn, iron accumulates at the nodes of the stalk which interferes with translocation of nutrients to the roots. In this situation the roots are weakened and become susceptible to soil fungi often resulting in root rot and consequent lodging of plants. A much more vigorous root system develops when soil potassium levels are high. In the foliar analyses of tomato plants showing the characteristic symptoms of virtue streak disease. Thomas and Mack (1941) found that infection was associated with a low level of nutrition, especially characterized by high levels of nitrogen and low levels of potassium.

7. *Maintenance of Turgor*

The potassium ion is also believed to be in part responsible for the maintenance of proper turgor of plant cells. In this respect, according to Hoffer (1938), potassium affects the colloidal cytoplasm and helps to regulate the degree of swelling and water economy of cells. Stoklasa (1936) has suggested that this property is important in increasing the resistance of plants to the dehydrating effects of frost and drought.

8. *Photosynthesis*

It has been suggested that potassium may be important in photosynthesis, since potassium deficiency commonly leads to reduced rates of CO_2 assimilation. However, as Watson (1947) has pointed out, the proof of increased efficiency of leaves is difficult to evaluate, because potassium fertilizers usually increase leaf surface areas, especially in the early part of the growing season.

In the past, several investigators, including Remy and Liesegang (1926), have reported that potassium influences the quantities of the chlorophyll components in plants. Though not entirely successful, Warburg (1919) attempted to correlate quantity of potassium with sugar production on the basis of energy quantities in light. It has been noted at Rothamsted and in Germany that potassium fertilizers on wheat are more effective in cool summers with little sunshine than during warm sunny seasons. Whether the effect of light can be separated from that of temperature and moisture is doubtful. T'Hart (1949) concluded that sunlight had little or no influence on the response of permanent grasses to variable potassium applications.

Proposals that radioactive emanations from naturally occurring radioactive potassium K^{41} in plants stimulate photosynthesis and other physiological oxidative processes have been advanced by Bruno (1928), Loew (1934), and Stoklasa (1934). Since potassium is the only radioactive element occurring in plants in appreciable quantities, these hypotheses are of special interest. Although germination of seeds and growth of sugar beets have been reported to be increased by exposure to beta and gamma radiation, photosynthesis occurs only under conditions of light. If radioactive emanations are important, this process should not be so dependent on light.

III. Potassium Deficiency Symptoms

Higher plants are normally green. Any condition which affects the metabolism of the plant will eventually influence the development of chlorophyll. Thus, starvation for any nutrient results in failure to produce chlorophyll, with the result that the foliage turns yellow. Time and pattern of yellowing and the plant part first affected vary for the different nutrients. In general, potassium deficiency is manifested first by a yellowing of the tips and edges of older leaves. As deficiency becomes more severe, the yellowed areas move toward the center and base of the leaves, and the younger foliage begins to show starvation symptoms. Potassium deficiency symptoms are characterized by a sharp contrast between the yellow and green areas of the leaves of many crops.

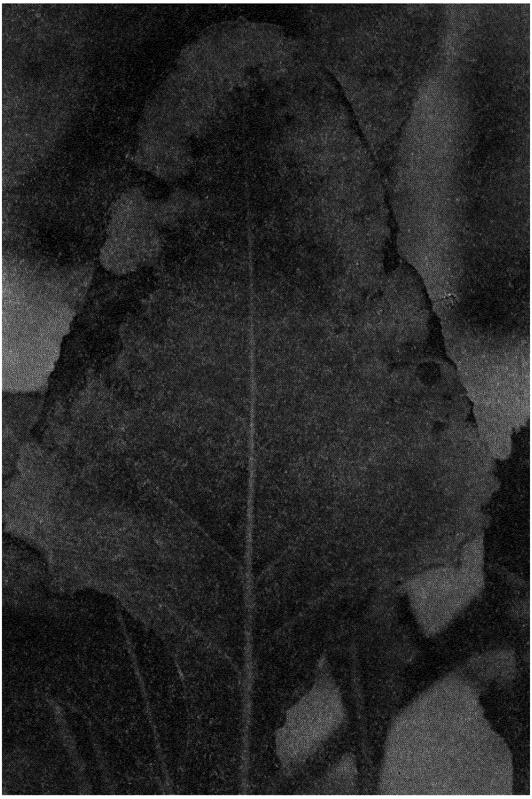

Fig. 1. Leaf from a potassium-starved sugar-beet plant. Note the yellowing tip and edges where necrosis has started.

In the later stages of potassium starvation, leaf edges become necrotic and the tissue disintegrates, giving the leaf a ragged appearance (Fig. 1). This condition is often called leaf scorch. Since potassium is considered to be a mobile nutrient within the plant, it can be translocated from the older to the younger tissues and organs very readily. Little evidence is available which indicates that the reverse trend occurs, although some workers have shown that potassium may move from maturing plants back into the soil.

Excellent reviews of potassium deficiency symptoms of the more common crops have been presented by Eckstein *et al.* (1937) and McMurtrey (1948). Color plates showing potassium deficiency conditions in a wide variety of plants are available in works by Wallace (1951), Cook and Millar (1953), and by McMurtrey and others (1949).

Crops can generally be grouped with respect to the type of deficiency symptoms they exhibit when the supply of potassium is inadequate. Some of the more extensive groups are the small grains and grasses, the clovers and alfalfa, the beet crops, the brassica crops, the bean and pea group, the tree fruits, and others. Marked starvation symptoms are shown by the plants in one group, whereas in others, the plants present only minor physiological disorders.

1. Grasses and Small Grains

In small grains and grasses, potassium deficiency symptoms are less striking than in many other crops. During late stages of potassium starvation especially, it is virtually impossible visually to diagnose this deficiency, since it may be confused with a shortage of nitrogen and complicated by the presence of diseases. The most common symptom indicating lack of potassium in small grain is termed "edge scorch," which starts with the yellowing of the tips of the lower leaves. There is a distinct tendency for the yellowing to proceed faster along the edges of the leaves than in the middle. However, the leaves are so narrow that this characteristic is likely to be unnoticed. In the later stages, the leaf margins turn brown, and the entire leaf may wither.

It has been noted that barley requires a higher level of potassium than wheat or oats and sometimes exhibits a specific symptom. An early sign of need for potassium in barley is the appearance of purplish spots even preceding the marginal firing of leaves. According to Cook and Millar (1953) these dark areas may persist even until maturity. Wallace (1951) points out that if the deficiency is acute in barley, the leaves become chlorotic and show white blotchy lesions.

In addition a shortage of potassium in the cereal grains may result in a bluish-green color of young leaves, excessive tillering, and shriveled and immature grain. The excessive tillering may be due to an excess of phosphorus to potassium.

2. *Corn*

Corn is commonly used as a plant to demonstrate potassium deficiency. The symptoms are very plain and not easily confused with the starvation signs of other nutrients. Marked signs of a lack of sufficient potassium for normal growth may appear at any time during the growing season, although the condition is most common after the plants are several weeks old. The first symptom in young plants is a decrease in rate of growth. Very soon the leaf tips of lower leaves become yellow, and this chlorosis proceeds in a streak along the leaf margins, which then turn brown. When the oldest leaves are entirely dead, the young leaves may be normal in color. In cases where the pattern of yellowing of the leaves is indefinite, the lack of potassium must be verified by the use of tissue tests. When plant potassium is low, tests for nitrogen and phosphorus in the green tissue will invariably be high. Other characteristics of potassium-deficient corn plants are weak stalks, stalks with short internodes, ears poorly filled at the tips, and a susceptibility to ear rot organisms.

3. *Clovers and Alfalfa*

Potassium deficiency in these legumes is easily recognized. The first visible manifestation of a need for potassium in clovers and alfalfa is usually the presence of small white dots together with yellowing at the tips and edges of the older leaflets. The white dots occur in a definite pattern, roughly parallel to the edges of the leaf. In many instances they appear before the yellow edges are apparent. The white dots are actually sunken areas, as if caused by a disintegration of the tissue between the upper and lower epidermis. As the deficiency continues, the yellowing extends over the entire leaf, and the margins turn brown and become necrotic. At this stage, the lower leaves may drop from the plant, and it appears as though the crop is suffering from a lack of moisture.

4. *Field Beans, Soybeans, and Cowpeas*

Nutrient deficiency symptoms appear quite similar on these three crops. Evidence of a potassium shortage may appear as early as the four leaf stage. As is true on most plants, the tips and edges of the leaflets on the older leaves turn yellow first. The yellowing then spreads gradually toward the center and base of the leaflet. This condition is followed by a necrosis and browning of tissue around the leaf margins. Since the center of the leaf grows at a normal rate, whereas growth along the edges is slow, a crinkling or cupping is usually evident. There is always a sharp contrast between the yellow and green portions of potassium-deficient leaves. Under acute conditions of potassium shortage, many leaves may drop from the bean plants in midsummer, giving the impression that the plants are maturing too rapidly.

5. *Sugar Beets and Mangels*

Sugar beets and mangels like many root crops contain rather large quantities of potassium, and therefore it is not surprising that a deficiency of this element is very soon reflected in the appearance of the plant. The older leaves which are affected first turn yellow at the tip and along the margins. As this condition works toward the center and base of the leaf, the edges become brown and necrotic. Sometimes the chlorotic area becomes yellowish grey rather than distinctly yellow, as is characteristic of potassium starvation in bean leaves. Another fairly reliable symptom is that the leaves tend to be long and narrow and the petioles may show brown longitudinal lesions.

6. *Potatoes*

The potassium requirements of white potatoes are very high, and this crop requires a continuous supply of the element for normal growth. When a deficiency condition exists, one of the first symptoms is that the growth of the plant is restricted and the internodes become short, resulting in a bushy appearance. Generally the leaves are smaller in this condition, lose their smooth surface, and become crinkled and bend downward. The younger leaves present an abnormally dark green to bluish-green color, which is considered to be a fairly reliable sign of potassium starvation, when associated with other disorders. As the deficiency becomes more acute, the older leaves turn yellow, followed by browning or bronzing of the leaf tips and margins. In some cases interveinal chlorosis has been reported along with considerable brown spotting of the under leaf surface. In severe cases, the leaf margins break down, and various parts of the stem and petiole become discolored, after which the plant collapses prematurely from lack of vigor. As might be expected, the roots and tubers are poorly developed, and their cooking quality is low.

It is generally agreed that darkening of potatoes is most frequently due to the oxidation of free amino acids and that any one of several factors may be responsible for accumulation of these compounds in the tuber. Numerous reports have been published suggesting that potatoes grown on soils low in available potassium commonly discolor on boiling. Mulder (1949) found an inverse relationship between potassium supply to potato plants and the content of free tyrosine in the tuber. It is well known that under favorable condition tyrosine can be converted by enzymatic action into black oxidation products.

7. *Tobacco and Cotton*

One of the important factors in production of quality tobacco is a plentiful supply of potassium in the soil. Insufficient quantities of potassium as indicated by specific symptoms have been noted throughout the entire growth period of this plant. If the need for this nutrient occurs in the early growth stages, the lower leaves of the tobacco plant show a typical mottling and chlorosis at the leaf tips and margins. This condition is rapidly followed by formation of necrotic spots within the mottled areas. These dead spots commonly enlarge and join to form larger areas, until most of the interveinal tissue presents a rusty brown appearance. Much of this dead tissue may fall out, giving the leaves a very ragged appearance. Those parts of the leaf not so affected take on an abnormally dark green color. It is interesting to note that if the deficiency symptoms develop after the plant is well grown, mottling may appear only on the younger or upper leaves without affecting the mature lower foliage to any great extent. Other potassium starvation signs include cup-shaped leaves, slender stalks, and a poorly branched root system.

Steinberg (1947) has concluded from field and laboratory studies with tobacco plants that symptoms of frenching are due to abnormal protein metabolism and excessive accumulation of metabolites. Marked increases in free amino acid content were noted in plants showing symptoms of various mineral deficiencies. When potassium was a limiting growth factor, the per cent increase was almost 600 per cent. These data were supported by experiments with seedlings grown in aseptic culture in which traces of free amino acids produced typical frenching-like symptoms.

The most striking symptom of potassium deficiency in the cotton plant is known as "cotton rust." This condition is the result of a progressive yellowish-white mottling around the leaf margins, whereby the normal green leaf turns light yellowish-green and yellow spots appear between the veins. The centers of these spots become necrotic. As the deficiency becomes more acute, these spots merge with the dead tissue around the edges of the leaf, which curl downward. The whole leaf finally becomes reddish brown in color, dries up, and is shed prematurely, leaving half-opened bolls which are dwarfed and immature.

Many bolls even fail to open, and the fiber is of poor quality. Nelson (1949) reported that the use of potassium fertilizer produced marked increases in boll weight, mean fiber length and weight, and per cent of mature fibers, whereas the per cent of lint was decreased.

8. Vegetable Crops

Many vegetable crops are grown on sandy or organic soils, both naturally low in available potassium. Since their requirement for potassium is quite high, nutrient deficiency symptoms are often observed. High-potash fertilizers are generally recommended for these crops.

The tomato plant presents somewhat similar symptoms as the potato when it is in need of potassium. Stunted growth, low yields, and crinkled leaves are preliminary indications that tomato plants are receiving insufficient potassium. As the disorder progresses, the older leaves turn grayish-green, with the development of a yellowing and finally a bronzing of the leaf edges. Some of the older leaves of relatively mature plants present a striking pattern of chlorosis, with interveinal tissue turning quite yellow in contrast to the green tissue near the veins. The scorched margins of the leaf tend to curl forward, as is typical with other plants. It has been reported that the yellowing in the earlier stages of the deficiency may be accompanied by the formation of white dots when soil nitrogen levels are high. Other evidences of a lack of potassium in tomatoes are the presence of slender stems, which become hard and woody, and a poorly developed root system.

Hester (1941a) reported that tomato fruits grown on soils low in available potassium are commonly low in sugars and ascorbic acid. Foliage is rapidly lost on potassium-deficient plants, exposing the fruit. Yellow-top fruits are much more prevalent on plants showing potassium deficiency, and loss in processing is much greater than with normal fruits. Harvey (1942) found that adequate potassium decreased cracking of the skin and gave smooth, firm fruits, which handle and ship well.

Potassium deficiency symptoms in cabbage, kale, brussels sprouts, cauliflower, and radishes are quite similar in pattern. In the early stages the borders of the leaves become bronzed. This bronzing may extend inward, but the most characteristic feature in cases of acute deficiency is the marginal browning or necrosis. Brown spots often develop in the interior portion of the leaf between the veins. The parts of the leaf not affected are commonly dark green and curled backwards, though not always so. Skinner (1949) noted that extreme potassium deficiency in radishes was exhibited by a deep yellow-to-bronze color of the lower leaves and stems. The leaves tended to be thick and leathery, and the roots were poorly developed.

In carrots, the need for potassium is first manifested by curled leaves and a squat growth. The tips and edges of the older leaves become brown first, followed by a fading of the normal green color, and finally a bronzing of the entire leaf. The affected leaves then collapse and die.

In cucumbers and melon plants a lack of sufficient potassium is indicated by marginal browning and necrosis. If the disorder continues, the browning may spread into the interveinal leaf tissue. The cucumber fruits are short and commonly have an enlarged tip end.

Lettuce plants starved for potassium first exhibit the characteristic browning of the margins of the older leaves. Later the entire leaf may become brown.

9. Deciduous Fruits

Symptoms of potassium deficiency have been reported on all types of deciduous fruit. Davidson (1949) and Wallace (1951) have presented valuable descriptions of physiological disorders resulting from a lack of potassium. Of all the representatives of this group, the peach has the greatest potassium requirement. Visual evidence of lack of potassium has been noted especially in peach orchards located on light-textured soils, on droughty shale and limestone soils, and on soils low in organic matter. Heavy liming of sandy soils has reportedly induced deficiency in peaches. Davidson (1949) stated that peach trees may show severe potassium starvation symptoms while apple trees in the same orchard show little need for this nutrient.

The first indication of need for potassium in peach trees is a crinkling of the leaves near the middle portion of the new growth. This crinkling, caused by uneven growth in the leaf blade, becomes more pronounced as the deficiency becomes severe and may result in a rolling of the leaves as well. Such rolling may be caused by other abnormal conditions, but then the leaf crinkling is not evident. A light red or purplish pigmentation usually develops on the lower surface of the longitudinally rolled leaves.

Since lack of potassium curtails nitrogen utilization, the leaves turn yellowish-green, and the tips of the new growth become stiff. Brown necrotic spots commonly develop, and these areas drop out to leave holes in the blade and along the margins. Whether the leaves drop off prematurely depends on the time of the season when the deficiency becomes severe. Davidson (1949) has noted that young peach trees grown in the greenhouse have undergone three successive cycles of leaf necrosis in one season. Fruit bud formation is markedly influenced by the supply of potassium. Peach yields may be sharply reduced even when deficiency symptoms on the foliage are relatively mild.

On apple leaves, the outstanding symptom of potassium starvation is marginal scorching. However, when the deficiency is not too apparent, it may be confused with symptoms indicating a lack of nitrogen. The resulting accumulation of carbohydrates and reduced nitrogen utilization in the early stages of this deficiency are commonly associated with a yellowish-green foliage and a yellow or red color in the twigs. Marginal foliage necrosis, evident when potassium starvation is not too severe, occurs near the middle of the current season's growth and gradually moves to the tips and base of the affected shoots. The brown scorching is usually preceded by a dark purplish discoloration caused by plasmolysis in which cell sap moves into the spaces between the cells. In cases of very severe potassium starvation necrotic areas may develop throughout the leaf area.

The translocation of potassium from affected tissues to regions of new growth enables deficient apple trees to make considerable linear growth, though it is usually slender in nature. A large number of fruit buds may develop and set fruit on trees growing under conditions of moderate potassium deficiency, but these fruit are likely to be abnormally small, subacid, and woody to taste.

The main symptom of lack of potassium in the small or bush fruit is marginal scorching. In strawberries the mature leaves of intermediate age are generally affected first. Necrosis is not always confined to the leaf margins. Usually the scorched leaves have a rather normal green color except for some purplish pigmentation near the necrotic areas. According to Wallace (1951) red currants and raspberries commonly show some interveinal chlorosis or browning in addition to marginal necrosis. In gooseberries and currants, purple tinting of the leaves tends to disappear as marginal scorching develops.

10. Citrus Fruits

Chapman *et al.* (1947) found that slight potassium deficiency in oranges was indicated first by a low content of leaf potassium. A slightly more serious deficiency was manifested by a slight reduction in the size of the fruit. Quality, however, was very good, the fruits being smooth, thin-skinned, juicy, and of good acid and total solid content. The vitamin content was normal. The fruit colored earlier than did that from normal trees. These workers found further that seriously potassium-deficient trees produced twisted, curled, and puckered leaves. They lacked chlorophyll but were not scorched on the edges. Dieback occurred, and new growth was weak. Roots were enlarged and stubby. Fruits were small but of good quality.

General agreement among workers indicates that as the potassium supply to citrus increases, the total acid in orange juice increases. In some cases potash fertilization has been reported as lowering, raising, or having no effect on total solids in citrus juice. Variables such as climate, variety, rootstalk, cultural practices, soil moisture, soil fertility level, and sampling techniques may account for variable response to potassium.

Reuther and Smith (1952) found that a high rate of potash fertilizer did not greatly affect yield, but did produce a high proportion of late-maturing, poorly colored, large fruit with a thick, coarse-textured rind and with a low content of total solids in the juice. Low potassium fertilization produced early-maturing, well-colored fruit with thin rinds and with a high content of total solids and low total acid.

IV. Potassium Uptake during Plant Growth

1. Accumulation of Potassium by Plant Roots

The accumulation of mineral nutrients by plants grown in soil involves various chemical and physiological processes outside and within the plant root, none of which are well understood. Some workers believe that the entry of cations into an ionic double layer associated with root surfaces and cell walls is the first step in ion accumulation by plant roots. Jenny and Overstreet (1939) proposed the concept of contact exchange between colloidal clay and plant root surfaces. Lundegardh (1940) found that the regions of root tips and root hair development had a higher negative charge than other parts of the root, but ascribed the seat of ion adsorption to the cytoplasm. Williams and Coleman (1950) reported that plant root surfaces possess cation exchange capacities which could be measured by the adsorption and release of various cations.

There has been considerable conjecture regarding the accumulation of inorganic solutes within plant roots and the permeability of cell walls to account for differential penetration of solutes into living tissues. Several of the suggested mechanisms include ionic exchange between solutions or by surface migration and a chemical union between cations and some protoplasmic constituent. Since the concentration of salts in growing plants is usually greater than in the substrate, accumulation of ions takes place against a concentration gradient. Thus, as noted by Broyer (1951), most investigators have felt that some mechanism must be present whereby energy expended in oxidative metabolism can be applied to the accumulation and retention of solutes in living cells.

The energy requirement has been postulated as necessary for the formation of high-energy specific protoplasmic constituents which combine with inorganic solutes at the outer extension of the cell protoplasm. Jacobson *et al.* (1950) proposed a hypothesis involving metabolically-produced binding compounds to account for potassium absorption, according to the following reaction:

$$K^+ + HR = KR + H^+$$

The rate of accumulation was dependent on the concentration of potassium ions in the substrate and on the quantity of free binding constituents (HR). The concentration of the potassium complex (KR), which also controls the reaction rate, was determined by the difference in rate of formation and utilization. Conditions favorable for metabolic activity, such as adequate aeration and temperature, thus favor formation of binding compounds and, in turn, potassium accumulation. Recently, Overstreet *et al.* (1952), using radioactive potassium as a tracer, have demonstrated that a given concentration of calcium may exert both a depressing and a stimulating effect on the absorption of potassium by excised barley roots. The depressing effect was interpreted as a result of competition for the binding compounds, and the stimulating effect was postulated as the result of calcium acting as a cofactor in the utilization of the potassium complex formed during adsorption. The transfer of this complex by diffusion or protoplasmic streaming to points within the cell is visualized by Broyer (1951), where, through some change in physiological processes, the binding constituent releases the inorganic member with a consequent release of energy to the solute.

2. Potassium Requirements of Plants during the Growth Period

a. Seedling Stage. According to Van Slyke (1932) most crop seeds contain from 0.4 to 1.0 per cent potassium. This quantity is sufficient for germination and very early development but will not long sustain growth. Buckner (1915) pointed out that not all the potassium in the cotyledons of corn and beans and in the tubers of potatoes moves into the seedling. Approximately 45 per cent of the total potassium of bean seedlings was retained in the exhausted and nonfunctional cotyledons. At this time the seedling leaves and stems contained 46 per cent, and the roots accounted for the remaining 9 per cent of the total potassium. In the case of corn seedlings, the cotyledons contained 20 per cent of the original seed potassium after they ceased to function. About one-third of the total potassium was in the leaves, and the remainder was distributed equally between the stems and roots.

Davidson (1926) carefully analyzed corn seedlings 18 days and 27 days after planting in soils to which no phosphate-potash fertilizer was added. At the time of first sampling he found that the seedlings had absorbed 8 to 10 times as much potassium from the soil as was originally present in the seed. A week later the seedlings had removed from the soil 25 times as much potassium as was in the seed kernels. These data point to a very rapid uptake of soil potassium by corn in the seedling stage.

b. Vegetative Growth Period. It is well established that the phase of rapid vegetative enlargement in most annuals is characterized by a progressive increase in the absolute amounts of inorganic elements such as potassium. The tobacco and potato crops present good examples of this trend. Grizzard *et al.* (1942) determined for tobacco transplants the average rate of potassium uptake at different stages of growth during two seasons. On the twenty-first day from transplanting, potassium was being absorbed at a rate of 0.1 pound per acre per day. A maximum rate of uptake of 1.75 pounds per acre per day occurred 49 days after transplanting, followed by a decline to 0.8 pound per acre per day after 63 days. A study of potassium uptake by the potato plant at various growth periods was made by Carolus (1936). In the first 50 days after setting the seed piece, 14 pounds of soil potassium was removed by the crop on an acre basis. Twenty pounds was absorbed in the next 10 days, and during the period between 60 to 80 days an average of 4 pounds of potassium was absorbed per acre per day.

As the amount of synthesized organic materials increases in the plant, the quantity of potassium on a percentage dry matter basis decreases, even though the total absorption of potassium continues, as with sugar beets, until near maturity. Loehwing (1951) has pointed out that early absorption is generally in excess of current needs if the potassium in the substrate is adequate. Luxury consumption during this period is usually followed by translocation of potassium in later stages of growth. Bartholomew and Janssen (1929) considered this redistribution to be an important process in plants. Gericke (1925) found that curtailing the potassium supply of wheat plants at a very early stage did not cause cessation of later growth. Data by Anderson *et al.* (1939) showed that potassium, nitrogen, and phosphorus commonly increase in plants at this time faster than do calcium, magnesium, or iron.

A study of the ash composition of upland rice was made by Gile and Carrero (1915) at various stages of growth. Eighteen days after seeding, the above ground part of the plant contained 4.07 per cent potassium. During the 123 days growing period, a gradual decline of the element on a dry matter basis took place, and at harvest time the crop analyzed only 1.85 per cent potassium. Fonder (1929) found a similar trend in alfalfa leaves and stems sampled at seven dates during the first and second harvests. A wide variation in per cent potassium in this legume grown on seven soil types existed at the first sampling date. At full bloom of both growth periods, values for plants from all locations fell between 1 and 2 per cent. Ulrich (1948) noted a continuous decrease in per cent potassium of petioles from recently matured grape leaves over a four-month growing season.

c. Flowering. Three fairly distinct stages of metabolism from germination to flowering have been noted by Loehwing (1951). During the third stage just prior to flowering a general internal redistribution of inorganic and organic compounds takes place. During blossoming or anthesis, a general reduction in anabolic activity occurs in most plants with further redistribution of inorganic elements. Reduced supplies of carbohydrates in roots at this stage may partly account for reduced potassium absorption. In some species a final, short acceleration of mineral uptake and synthesis of organic compounds may take place. Burd (1919) noted that a distinct drop in total potassium for two weeks after heading of barley plants was followed by a short period of increased potassium absorption, and finally by a loss at maturity. It has also been noted by Hall (1949) that a transitory excretion of potassium and nitrogen occurred during blossoming of cotton plants grown in nutrient culture.

d. Seed or Fruit Formation. Many investigators have found that during the early stages of fruit or seed formation there may be a marked increase in mineral absorption by roots as well as an accelerated metabolism in the younger tissues of the plant. Mason and Maskell (1931) noted a substantial gain in potassium and nitrogen in cotton plants during that period. However, the main physiological change at this stage involves the diversion of inorganic and organic reserves to reproductive organs. As an example, Smith and Reuther (1950) concluded that a reduction in the absolute amount of potassium in orange leaves in late summer and fall was due to translocation to the fruit. Eaton and Joham (1944) reported that mineral uptake during boll formation of cotton plants rapidly declined or became negligible. Much of the decline in absorption of soil potassium during heavy fruiting was attributed to reduced movement of carbohydrates to the roots. An adequate supply of potassium has been found essential to secure a high rate of set in the navy bean (Fig. 2). Results of defloration experiments by Arnon and Hoagland (1943) indicated that developing tomato fruits draw on the potassium reserves of the leaves. Two general mechanisms were envisaged which bring about potassium withdrawal from older tissues. The first is a physiological change in old tissues incited by some hormone-like substance. The second hypothesis suggested that young tissues have the greatest retention of potassium from phloem. It is apparent from the rather uniform composition of seeds and fruit that these tissues are selective, since the mineral composition of the vegetative plant parts from which they are supplied is often quite variable, as shown by Arnon and Hoagland (1943).

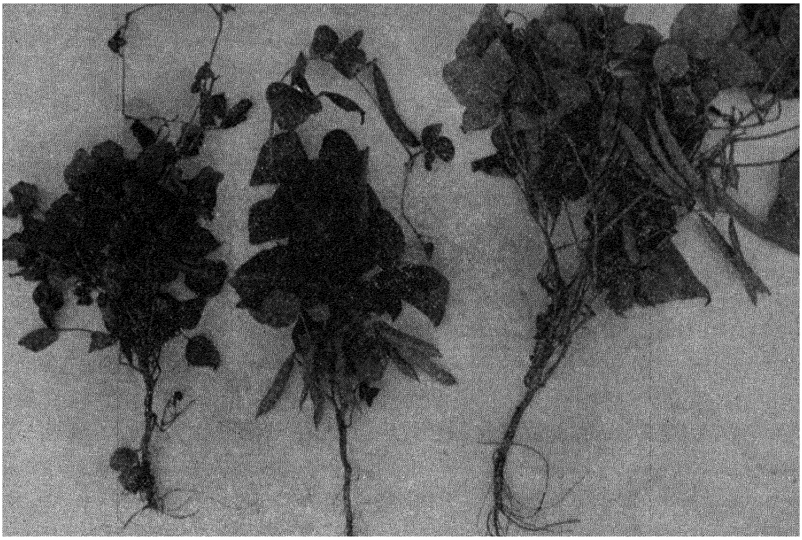

FIG. 2. Navy beans set more pods where potash was applied. Left—0-16-0, 300 pounds per acre, 2 pods. Center—0-0-8, 300 pounds per acre, 9 pods. Right—0-16-8, 300 pounds per acre, 14 pods.

3. *Transfer of Potassium from Plants to Soil at Maturity*

Absorption of soil potassium by plants is considered to require energy produced in root respiration. On the other hand, the transfer of potassium from plant roots to soil is a simple diffusion process. In order for roots to hold this uncombined ion against a decreasing concentration gradient, they must be in an active metabolic state.

Loss of some potassium, accumulated in cereals and tobacco during the growing season, has been noted by Burd (1919), Deleono (1932), and others during the period of maturity. The death of some foliage and consequent leaf drop is responsible for a portion of this deficit. However, this loss is believed to be mainly due to excretion from the roots to the soil, although complete recovery of a root system from soil is impossible. Chemical analyses by Knowles and Watkins (1931) of the top growth of wheat at different periods showed that the total quantity of potassium decreased shortly after heading. Assimilation of calcium followed a similar trend, but nitrogen and phosphorus increased during the main part of the growth period and then remained constant up to harvest. Though no root recovery was attempted, these data indicate a loss of about 50 per cent of the absorbed potassium into roots or to soil. No evidence has been presented to support the hypothesis of excretion of potassium from legume hays or grasses during periods in which hay is harvested.

Recent work by Jenny and Overstreet (1939) and Jenny *et al.* (1939) has shown that there is a continuous exchange between nutrient ions in soil and in plant roots. Low-salt barley plants growing in sodium-saturated clay suspensions lost potassium rapidly, but in potassium- and calcium-saturated clay systems this loss was only 60 and 10 per cent, respectively. This phenomenon is in direct contrast to the fact that barley roots placed in sodium chloride or water solutions lost no potassium, whereas in a potassium chloride solution, an appreciable transfer of root potassium to the solution was noted.

V. Potassium Requirements of Various Crops

1. *Variability of Plant Species*

The potassium content of plant tissue varies widely with species. Other factors causing variation are the level of exchangeable potassium in the soil, the quantity of other nutrients, physical conditions such as soil moisture and aeration, and the variety of the species. Variation in potassium content of different plants has been amply demonstrated in both water culture and soils.

Collander (1941) grew 20 plant species representing different ecological types and taxonomic groups in water cultures. Potassium and rubidium contents varied from 2 to 3 times the minimum value, whereas sodium and manganese ranged from 20 to 60 times the minimum. Newton (1928), working with sunflowers, beans, barley, and wheat in both water culture and soil, concluded that uptake of potassium was greater in culture solution and was less variable than when soil was used as the substrate. Drake and Scarseth (1939) found that 12 crop plants differed markedly in ability to remove potassium from soils with a low available supply. The response of these plants to added potassium was almost inversely proportional to their abilities to absorb native soil potassium. According to Lewis and Eisenmenger (1948) plants in lower stages of evolution utilized considerably more potassium from both soluble potassium salts and from ground orthoclase than did plants in the higher stages of development. This trend held for 22 seed plants in both the monocotyledon and dicotyledon groups.

Cooper *et al.* (1947) have attached considerable significance to certain physiochemical properties of cations, such as standard electrode potentials and ionization potentials, in explaining the chemical composition of crop plants. Potassium is considered to have the highest intensity of ion formation, followed by sodium, calcium, magnesium, aluminum, manganese, and iron. A close relationship between the relative strength of ions and the quantity of nutrients in plants has been pointed out. However, a process of selective absorption is needed to explain the accumulation and exclusion of certain nutrients in various plants.

The factors that control absorption of cations by plants are numerous and the reasons for differences in mineral composition of plants are not clearly understood. It was suggested by Mattson (1948) that the uptake of cations by different plant species might be controlled in part by the cation exchange capacity of the colloid fraction of plant roots. The results of work by Elgabaly and Wiklander (1949) indicated that the greater the cation exchange capacity of the root, the greater would be the divalent/monovalent ratio in the plants. Using an electrodialysis technique, Drake *et al.* (1951) measured the cation exchange capacity of roots of a number of agricultural plants. He found dicotyledonous plants to have higher values than monocotyledonous plants.

2. *Percentage Composition*

The average percentage potassium composition of most agronomic and horticultural crops has been listed by Van Slyke (1932), Morrison (1949), and Beeson (1941). Although the data do not indicate the ranges within which this element may vary under different levels of soil fertility, they are valuable, together with field weights and dry matter yields, in an evaluation of the potassium requirements of plants. In some cases the average values of potassium on green weight and dry weight bases given by different workers are not similar. Such deviation is probably due to differences in crop varieties, stage of plant maturity, soil areas from which crops were sampled, and moisture content of plant material at time of analyses.

The legume hays have the highest potassium content of any group of agricultural crops. Most values for alfalfa, sweet clover, and vetch range between 1.75 to 2.0 per cent potassium. Results by Morrison (1949) for Ladino, alsike, and crimson clovers fall between 2.4 and 2.8 per cent and are almost twice as high as those listed for red clover. Data by other investigators, however, show these clovers and cowpeas to have a potassium content varying from approximately 1.0 to 1.7 per cent. Of the legume hays, soybean and lespedeza contain the lowest concentration of this element, commonly averaging between 0.7 to 1.0 per cent potassium.

Most of the common grasses, unless heavily fertilized with potash salts or manure, contain from 0.8 to 1.5 per cent potassium. A wide variation can be noted in the content of red top and timothy hays as listed by Van Slyke and Morrison. The latter worker has listed an average potassium content of 2.35 per cent for brome grass, which seems high. His analysis for alfalfa-brome hay of 2.2 per cent, however, agrees with data which show high potassium absorption by this crop mixture.

In corn and small grain crops most of the plant potassium is found in the straw or stover. Van Slyke (1932) and Romaine (1940) report about three times as much potassium in the stems of these plants as in the seed. The seed of these crops remains quite uniform in potassium content under different soil fertility levels, whereas that of the straw fluctuates widely. Lucas *et al.* (1942) suggest that, because of this, analyses of wheat straw and corn stover are more valuable in a study of potassium relationships than are tests of grain. The common cereal grains, including buckwheat and sorghum, contain from 0.3 to 0.5 per cent potassium, whereas the straws contain from 0.5 to 1.5 per cent. Peanut hulls and cottonseed hulls are also high in potassium. According to both Van Slyke and Morrison, oat and barley straws contain significantly greater amounts of potassium than do wheat, rye, or rice straw. Analyses of flax seed show this seed crop to be about twice as high in potassium as are barley and oats.

Large-seeded legumes such as soybeans, cowpeas, velvet beans, field peas, and field beans usually contain from 1.0 to 1.5 per cent potassium. It is interesting to note that the seed of these crops contains from two to three times as much of this nutrient as does the straw.

It is well known that the root and tuber crops are heavy feeders on potassium. Fertilizer recommendations have long attested to this fact. Actually the potassium content of roots and tubers on the field weight basis is relatively low. Sugar beets, mangels, white and sweet potatoes, rutabagas, and turnips all contain from 0.3 to 0.5 per cent potassium. The top material of these plants usually has a composition quite similar to the underground parts. High potassium utilization is the result of large dry matter yields.

Of all the economic crop plants, none contain so much potassium per unit dry weight as tobacco. The leaves and stems of this plant commonly contain over 5 per cent. Considerable data are available relating the burning quality of tobacco to the potassium content of the leaf.

The sugar-cane plant contains between 0.3 to 0.5 per cent potassium Molasses extracted from sugar cane and sugar beets in the sugar refining process is about ten times higher in potassium than is the entire plant.

Data are presented by Van Slyke (1932) on the potassium content of the more common tree fruits and small fruits. Apricot and currant fruit have the highest per cent potassium, whereas the apple and pear show the lowest values. Leaf potassium is highest in currants and apricots and somewhat lower in the foliage of apple, grape, pear, and quince. Data by Kenworthy (1953) show no appreciable differences between the potassium content of the leaves of apple, pear, peach, and cherry. No large differences in the potassium content of new wood is noted for any of the fruits. These values are in accord with leaf potassium contents listed by McCollam (1952). Van Slyke (1932) presents no values for citrus fruit leaves, but McCollam's data indicate they would generally contain from 0.3 to 0.7 per cent potassium.

Many weeds are higher in potassium than agricultural plants. Singh and Singh (1939) determined the potassium content of 49 weed species grown under natural conditions on the same soil. Weeds rich in potassium included nine species in the Capparidaceae, Portulacaceae, Chenopodiaceae. Compositae, and Amaranthaceae families with an average content of 3.3 per cent at the preflowering stage. Blaser and Brady (1950) found that the potassium content of Ladino clover, grasses, and weeds grown together was in the relative order of weeds > grasses > clover, regardless of the amount of potash fertilizer applied. Vengris *et al.* (1953) and Lucas *et al.* (1942) also reported that many common weeds were higher in potassium than were the associated red clover plants.

3. *Requirements for Good Acre Yields*

The total potassium requirement of a crop is a function of the potassium content of the various plant parts and the dry weight produced in a single growing period. Thus this value is not always directly related to the potassium content. The roots of most crops are not included, since it is virtually impossible to make a quantitative recovery. A compilation of the amount of potassium used by various crops as given by Van Slyke (1932) and Romaine (1940) necessitates the use of average figures for yield and chemical analysis.

Good acre yields of alfalfa and sweet clover require from 100 to 130 pounds of potassium, whereas for red clover, crimson clover, soybeans, cowpeas, and vetch, the probable requirement is 50 to 75 pounds. The grasses remove considerably less potassium than do legumes, largely because of lower dry matter yields. In one and one-half tons of dry hay of Kentucky blue, orchard, fescue, rye, redtop, and timothy grasses there will be from 25 to 45 pounds of potassium. The latter two grasses commonly contain less than Kentucky blue, orchard, and fescue grasses.

The cereal grains contain about the same amount of potassium as the grasses, but corn removes almost two times as much. Acre yields of oat (50 bu.) and barley (40 bu.) crops require from 30 to 40 pounds, wheat (30 bu.) and rye crops (30 bu.) require from 25 to 35 pounds, buckwheat (20 bu.) requires 50 pounds, and corn (60 bu.) contains 50 to 70 pounds of potassium. In corn, oats, and buckwheat, the ratio of the amount of potassium in straw or stalks compared to that in grain is about 4/1, 3/1, and 18/1, respectively.

As previously mentioned, tuber and root crops usually have a high requirement for potassium. Romaine (1940) stated that a 300 bushel per acre crop of white potatoes and sweet potatoes would remove 140 and 96 pounds of potassium, when roots or tubers plus vines are analyzed. A 15-ton crop of sugar beets accumulates about 120 pounds, and good acre yields (10 tons) of turnips and rutabagas will commonly contain 100 pounds per acre, when the entire plant is considered. In most cases the roots or tubers contain approximately twice as much potassium as the aerial portion of these plants.

A good cotton crop, yielding 500 pounds of lint per acre, contains from 30 to 40 pounds of potassium. The burrs, leaves, and stalks contain about two and one-half times as much as the lint and seed combined. Tobacco is a crop considered to have a high potassium requirement. Approximately 100 pounds of this nutrient element is needed for a crop with a leaf yield of around 1500 pounds per acre. Haley and Reid (1943) stated that a crop of flue-cured cigarette tobacco requires only half the potassium needed to produce a cigar tobacco crop grown in the Connecticut Valley. Sugar cane does not remove as large quantities of potassium from soils as many other crops having less total dry matter. According to Van Slyke (1932) an acre yield of 30 tons of green stalks, leaves, and tops will remove only 36 pounds of potassium.

The amount of potassium in fruit, foliage, and new wood of fruit trees in full vigor will depend largely on fruit yield, the number of trees per acre, and the variety sampled. For peaches this value will range between 60 to 80 pounds per acre; for apples and cherries from 15 to 30 pounds per acre; for pears and grapes from 20 to 30 pounds per acre; for plums from 30 to 40 pounds per acre; and for oranges about 100 pounds of potassium per acre. Good acre yields of raspberries, blackberries, strawberries, and currants will remove from 10 to 20 pounds of potassium when all new growth is included.

4. *Effect of Varietal Difference*

The influence of crop variety on the absorption of soil potassium may be extensive. Though little knowledge is available regarding reasons for varietal differences in feeding power for mineral nutrients, most workers believe such differences can be explained on the basis of some property of the root system. Greater variation in mineral composition may sometimes be found within varieties of a crop grown on the same soil than between plants of unrelated species.

Mach and Hermann (1934) noted that the potassium content of the vines of three varieties of potatoes was widely different, whereas the composition of the tubers was quite similar. Eckart (1905), working with 12 varieties of sugar cane, found over 100 per cent variation in the potassium content of stalk material and 80 per cent differences in the leaves and tops. Woodford and McCalla (1936) studied the uptake of potassium and other nutrients by two varieties of .wheat in Alberta. Significant differences in the potassium content of the wheats were noted at four dates of sampling at one soil location and at two dates at another soil area. In another instance, differential response to potassium, nitrogen, and phosphorus by three pure-line varieties of barley was determined by Gregory and Crowther (1931). Two years data at Rothamsted supported the conclusion that these varieties differed widely in their efficiencies in use of potassium supplied at a low level.

In studies of the nutrition of apple trees, Batjer and Magness (1938) obtained higher percentages of potassium in leaves from DELICIOUS apple trees than from those of ROME BEAUTY and YORK varieties. Smith and Reuther (1949) reported highly significant differences in the leaf potassium content of Valencia oranges from six different rootstocks. Significant differences in the potassium content of four varieties of celery grown on muck soil were noted by Laughlin (1947). The SUMMER PASCAL variety averaged 17 per cent more potassium than did the yellow varieties. This worker also found appreciable variation in the amount of potassium absorbed by three varieties of sugar beets commonly grown on organic soils. Nelson *et al.* (1945) found that increasing amounts of potash fertilizer markedly increased the potassium content of one variety of soybean seed but had little effect on two other varieties.

It has been pointed out by Browne (1938) that the amount of potassium utilized by several varieties of a given crop may be markedly affected by the soil type on which it is grown. For example, five varieties of sugar-cane seedlings grown on four different Florida soils absorbed widely different quantities of potassium, depending on the soil involved. A variety which contained the highest per cent potassium when grown on an organic soil contained the lowest percentage on the other soils.

Numerous observations have been made noting a display of potassium deficiency symptoms on one crop variety, while an adjacent variety appeared normal. Watson (1949) reported this condition in greenhouse experiments with two tomato varieties grown under similar conditions. Both varieties at a low fertility level were stunted and contained similar amounts of leaf potassium; yet one variety exhibited marked potassium deficiency symptoms while the other remained green. These data suggest a more efficient utilization of potassium by the plants of one variety.

5. *Competition in Plant Associations*

When two or more plants grow in close association, competition for nutrients, moisture, and light often results. This relationship may exist between weeds and crop plants or between various types of agronomic crops themselves. The degree of nutrient competition will depend on the plant species in association, the population of these plants, and the supply of available nutrients. Root distribution patterns and the supply of soil moisture at various soil depths will markedly influence competition for nutrients. Nitrogen and phosphorus are most generally needed by grasses, whereas legumes are most responsive to applied phosphorus and potassium.

Agronomists have known for some time that adequate potassium fertilization is needed for the maintenance of legume stands where available soil potassium levels are not high. Jackson *et al.* (1947) found that potash added to a well-limed and phosphated soil increased the percentage of alfalfa in second year hay from practically none to over 35 and increased alfalfa plus clover to over 50. These workers emphasized the need for continual replacement of potassium as a top-dressing on established forage stands to help maintain a high proportion of legumes. A similar conclusion was reached by Rich and Odland (1947) who conducted experiments to determine the effect of various fertilizers on the yield and botanical composition of legume-grass hay. A reduction of annually applied K_2O from 100 to 50 pounds per acre lowered the proportion of legumes four years after seeding from 50 to 3 per cent and the yield from 3.1 to 1.6 tons per acre. Prince *et al.* (1942) have pointed out that in New Hampshire potassium was the most important element for increasing the longevity and yield of alfalfa stands. Investigations by Sprague and Eby (1948) showed that additions of potash to many New Jersey soils encouraged the spread and survival of Ladino clover.

Blaser and Brady (1950) reported on the competition for potassium exhibited by weeds, grasses, and legumes in New York. When available soil potassium was low, the relative intake of potassium by these plants was in the order of weeds > grasses > legumes. The fact that cultivated grasses start their growth in the spring earlier than legumes in this region allows them first opportunity for absorption of soil potassium. Since the root distribution pattern of clovers, especially Ladino, and grasses are quite similar, these legumes may suffer from lack of potassium. Although the use of nitrogen generally reduced the per cent potassium in grasses and weeds, the total amount of potassium removed was greater because the growth of nonlegumes was stimulated. Potassium fertilizer increased the growth of legumes but did not directly affect the nonleguminous plants. Most weeds are high in potassium, as indicated by work of Singh and Singh (1939) in which 49 species of weeds grown under natural conditions were found to be considerably higher in potassium and other mineral nutrients than most common crop plants.

Drake *et al.* (1951) proposed a working hypothesis regarding competition for potassium between legumes, grasses, and weeds. They stated that leguminous plants which have root systems with high cation exchange capacities absorb cations such as calcium and magnesium with much greater energy than they do the monovalent cation potassium. Conversely, the grasses and many weeds with low exchange capacity roots absorb potassium with greater ease than they do the divalent cations. On this basis, crops like red top, timothy, Kentucky blue grass, and brome grass can obtain sufficient potassium from soil where the available supply is low. Alfalfa, clovers, and soybeans, on the other hand, require a high level of available soil potassium in order to compete successfully with weeds and grasses.

VI. Effect of Soil and Climate Factors on Potassium Absorption

1. Soil Aeration

It is well known that oxygen or proper aeration is required for normal root growth and absorption of nutrients by roots. Fundamental advances in the nature of salt accumulation by plants were first made by plant physiologists about 20 years ago. For instance, work by Steward *et al.* (1936) showed that energy from aerobic respiration of living plant cells is necessary for the absorption of salts from solution. At the same time Hoagland and Broyer (1936), using excised barley roots, were able to prove that a high level of aerobic metabolism involving the presence of oxygen is required for absorption of salt against a concentration gradient. The need of oxygen for nutrient absorption was also emphasized by Arnon and Hoagland (1940) in studies with aerated and nonaerated solution cultures with actively growing tomato plants. These workers found that about 40 per cent more potassium was taken from aerated than from nonaerated cultures. Hopkins *et al.* (1950) demonstrated that the accumulation of radioactive potassium in tomato, soybean, and tobacco plants was proportional to log pO_2 from 0.5 to 21 per cent oxygen. Similar evidence of the importance of aeration in potassium uptake by corn plants was noted by Chang and Loomis (1945). However, these investigators concluded that the role of carbon dioxide toxicity had been overlooked in aeration studies. Additional solution culture work by Pepkowitz and Shive (1944) does not confirm the fact that potassium is one of the nutrients the uptake of which is most markedly dependent on dissolved oxygen supply. An extended review of work on the general subject of aeration and nutrient absorption by plants has been written by Hoagland (1944) and Broyer (1951).

It has been pointed out by Page and Bodman (1951) that direct information on the effect of soil aeration on nutrient availability is rather scarce. This lack of knowledge is mainly due to inadequate methods for characterizing soil aeration. Recently, however, several new techniques, including the platinum microelectrode developed by Lemon and Erickson (1952) to measure oxygen diffusion, should give valuable information in future studies involving nutrient absorption from soils.

Few greenhouse experiments have been designed to study plant absorption of potassium as affected by various degrees of soil aeration. Lawton (1945a) was able to show that the potassium content of corn plants grown on compacted soils and on soils in which moisture contents were very high was significantly lower than that of plants grown under more normal conditions. He found that potassium deficiency symptoms developed in plants when the soils were compacted or waterlogged and that such symptoms could be correlated by intermittent forced aeration. In this study the absorption of potassium was more closely related to soil aeration levels than was that of nitrogen, phosphorus, calcium, or magnesium. These data are in agreement with the results of several experiments conducted in solution culture. It is important to note that these soils contained levels of exchangeable potassium considered fully adequate for normal field growth of corn.

Vlamis and Davis (1944) studied potassium absorption by tomatoes, barley, and rice plants grown in a clay soil under conditions of normal and poor drainage. Decreased growth and reduced concentration of potassium in the plant sap of barley and tomato plants resulted from poor drainage. Solution culture experiments using various levels of oxygen confirmed the fact that the oxygen requirements of the three crops are markedly different. Either the rice plant can carry out its internal processes at lower oxygen levels, or there is transport of oxygen from the shoot to the root of the plant.

2. *Excess Soil Moisture*

Under field conditions plant growth and absorption of nutrients may be affected where high soil moisture, compaction, or incorrect tillage practices have caused inadequate soil aeration. Few field data have been published relating the effect of high soil moisture on the inability of crops to absorb available potassium. Cook and Millar (1953) note that during cold, wet periods in the early part of the growing season potassium deficiency is common in white field beans and soybeans. In many cases, these symptoms disappear when air temperatures rise and excess moisture is drained away within a short period. Lawton (1945b) reported that potassium-deficient corn was found on several Clyde soils containing an adequate level of exchangeable potassium. These soil areas were poorly drained, and soil moisture was in excess during the first month after planting.

3. *Compaction and Tillage*

Since soil compaction is closely associated with tillage of soils, these topics are combined for discussion. Evidence of the reduction of availability of soil potassium due to tillage was first reported by Bower *et al.* (1944). These Iowa workers reported that corn grown on plowed plots was much less deficient in potassium than plants on listed, disked, or subsurface-tilled Fayette, Clarion, and Webster soils. Their chemical analyses showed that for the three soils studied an average of 1.8 per cent potassium was found in corn plants from plowed plots, whereas the potassium content of plants from subsurface-tilled areas tested only 1.3 per cent. Since the exchangeable potassium level in all plots of the same experiment was very similar, the effect of tillage was considered to be indirect and related to soil aeration.

A more extensive comparison of tillage practices in Iowa was conducted by Lawton and Browning (1948). At four of seven locations plowing resulted in corn plants with greater dry weight and higher potassium content than did other tillage practices. These workers concluded that on soils with favorable structure and well supplied with exchangeable potassium, little difference can be expected in potassium content and yield of corn from different tillage practices.

A number of other investigators have also noted that a lack of both potassium and nitrogen for normal growth of corn sometimes occurs under such tillage practices as disking or subsurface tillage. In Ohio, Page *et al.* (1946) observed over several seasons that corn plants on the unfertilized area of disked plots showed very severe potassium deficiency symptoms. In contrast no potassium starvation was found in corn where the moldboard plow was used. Additional data by Tyson and Crabb (1952) indicate that in five out of six years on a sandy loam soil severe potassium deficiency signs developed during late summer in corn on stubble-mulched plots. These observations were supported by plant tissue tests which showed that corn from plowed plots had an ample supply of potassium. On the other hand, Moody *et al.* (1952) did not find that mulch tillage increased the occurrence of nutrient deficiency symptoms in corn. Mulching, in these Virginia experiments, was accomplished by the use of a double-cut plow in contrast to subsurface sweeps used by Iowa and Michigan workers. Differences in potassium content of mature plants grown under the two tillage treatments were significant in 1948 and 1949, but were not consistent.

In recent years considerable interest has arisen regarding the lack of response of corn to deep placement of complete fertilizers in the Corn Belt. Some workers consider conditions of poor soil aeration to be a limiting factor in growth and nutrient absorption. A report was made by Hoffer (1945) that corn plants on certain soil areas in several Midwestern states in 1944 failed to respond to high fertilizer application in the plow furrows. Using ferrous-ferric iron tests to measure the depth of oxygen penetration from the soil surface, it was shown that the supply of oxygen in the root zones of most nonresponding soils was insufficient to keep roots alive and actively absorbing such plant nutrients as potassium.

4. *Gross Climate*

Climatic factors may have an important effect in controlling the mineral composition of crops. Although the plant is dependent on soil for its mineral nutrients, many of the physiological processes such as photosynthesis, respiration, and assimilation are significantly modified by differences in temperature, rainfall, humidity, light intensity, and altitude. These variations, in turn, may affect both mineral and organic components in plants.

Several studies have been conducted of the over-all influence of climate on the mineral composition of crops. LeClerc and Yoder (1912) reported the effect of climate at three locations in the United States on the mineral composition of wheat. Soils from California, Kansas, and Maryland were exchanged and TURKEY variety of wheat grown at all sites. Wheat grown on Kansas soil in California, Kansas, and Maryland contained 2 52, 2.80, and 2.28 per cent potassium, respectively. Similar differences were noted in wheat grown on the other soils at the locations involved.

In some areas, large variations in climate prevail over short distances. In a soil exchange experiment involving the growth of sugar cane at two locations several miles apart in Hawaii, Borden (1936) showed that 28 per cent more potassium was found in cane grown at one site than at the other. The main difference in climate at the two sites was precipitation.

It is a well-known fact that the effect of potash fertilizers on crops in cold, rainy summers with little sunshine is greater than in warm, sunny years. The results of two experiments by T'Hart (1949) on permanent grassland on peat soil, involving different rates of top-dressed potash, showed that the response of grass to these top-dressings depended on the temperature during the growing period. The differential effect of several seasons on the mineral composition of crops grown on the same soil has often been noted. Stubblefield and DeTurk (1940) reported a wide fluctuation in the potassium content of oat and wheat straw during the period 1936 to 1939. The effect was most pronounced with soils in a high state of fertility. Boynton and Compton (1945) showed that the potassium content of apple leaves from trees in 148 orchards varied significantly between 1941 and 1942.

5. *Limited Soil Moisture*

The study of nutrient absorption from dry soils has not received much attention. Most available evidence indicates that plants can absorb small quantities of nutrients from soils in which the moisture content is below the permanent wilting point. However, according to Richards and Wadleigh (1952) this source is probably inadequate for vigorously growing plants. Volk (1947) also presented data indicating that corn roots can remove potassium from soil at or below the wilting percentage. Corn plants which had part of their roots in contact with dry soil absorbed 70 per cent more potassium than did plants grown in potassium-free sand.

Also evidence that wheat seedlings were able to absorb potassium from soil in a similar moisture condition has been reported by Breazale (1930). In this study moisture was available to another part of the root system, and it is believed that the moisture content of the dry soil was increased by a transfer of moisture through the plant.

Under some conditions the nutrient composition of plants on a percentage basis increases when the soil moisture supply is low. In addition dry matter yields are reduced. Such evidence is presented by Emmert (1936), who conducted greenhouse experiments on two fine-textured soils to determine the effect of soil moisture level on nutrient uptake by tomatoes. Under dry conditions the plants were stunted and the fruit small with considerable blossom end rot. The potassium content of the fresh tissue of plants grown under a limited moisture supply was 15 to 25 per cent higher than in plants from the wet benches. Since the concentration of the cell sap increased only 1 to 2 per cent, no explanation was given for this consistent increase in plant potassium under conditions of drought.

It has been generally observed that potassium deficiency symptoms in various crop plants are most severe in times of drought. Some workers attribute this condition to restricted root growth and nutrient absorption, especially with respect to the more easily desiccated root hairs and rootlets. Other workers such as Wadleigh and Richards (1951) concluded that the relatively low potassium content of plants subjected to low soil moisture levels is related to the increased intensity of potassium fixation under such conditions. Chemical studies of the unavailability of potassium by Volk (1934) showed that dehydration was directly involved. However, work by Martin *et al.* (1945) suggested that the effect of drying on reduced availability of potassium is due to an increased concentration of ions at the adsorption interface.

6. *Temperature*

Little is known regarding the effects of temperature on the absorption of mineral nutrients by plants. Temperature, as a factor in growth, affects the metabolic activity and thereby the uptake of nutrients. Within this relationship, factors such as cell permeability, rate of root respiration, and rates of translocation and utilization may be influenced. Most workers have concluded that salt absorption is reduced under low environmental temperatures.

Hoagland and Broyer (1936), in controlled culture solution studies with excised barley roots, found that the concentration of potassium in the cell sap was approximately four times as high at 30° as at 10° C. Within the range of 10° to 25° C., potassium absorption was a direct linear function of temperature. These workers also calculated the accumulation ratio for potassium at various temperatures. This value, which represents the ratio of the concentration in the sap divided by the concentration in the solution, was dependent on the latter, but always increased as temperatures were raised within the range studied.

VII. Potassium from Organic Mulches Applied to Soils

1. *Types of Mulches*

Organic mulches employed as surface soil covers are used in agriculture for a number of purposes in orchards, forest nurseries, dry-land areas, eroded areas, greenhouses, and truck crop areas. They may be a part of soil management practices designed to control soil erosion, conserve soil moisture, improve aeration and porosity of soils, reduce weed competition, and supply certain nutrient elements for plant growth. It may be that a plant mulch is any plant material which is artificially placed on the soil surface. These are largely residues of crops which are grown elsewhere but may include such residues as straw, stalks, or hay left to remain after a crop is grown. Common mulch materials include grain straw, stalks, green residues such as legume and grass hay, sawdust, ground corncobs, forest litter, and peat as well as discarded products from the vegetable and fruit processing industries.

Such mulch materials are largely composed of the structural parts of plants, and as mentioned in the section on plant composition, they contain appreciable quantities of potassium. Since the potassium ion does not enter into any permanent organic combination in plant tissue, it can be readily leached from nonliving plant tissue. Many data are available to indicate that the more soluble fractions of soil potassium are often markedly increased through the practice of mulching.

2. *Soil Potassium Level*

At the present time mulches are being used to a considerable extent, together with cover crops and sods, in the production of fruit crops, both in pomology and small fruit culture. Gourley (1941) found that soil potassium under peach trees was very high after continuous mulching, even though no commercial fertilizer had been applied. A similar trend was noted by Kenworthy (1954), who found that soil samples under various mulches in a cherry orchard increased markedly in available potassium. Soil under an alfalfa mulch was five times higher than that having no mulch and 50 per cent higher than that under a straw mulch. In experiments conducted with raspberries, Boller and Stephenson (1948) found that the 0- to 6-in. depth of soil under ten years of a continuous straw mulch contained about two and one-half times as much soluble potassium as that which was not covered with mulch. A simulated mulch study by Harley *et al.* (1951) using orchard grass hay not in contact with soil showed that 30 pounds of potassium was released per ton of air-dry hay over a one-year period.

3. Plant Potassium Level

Studies conducted by Baker (1948) with potassium-deficient peach trees growing on a sandy soil showed that leaves from terminal shoots increased in potassium from 0.33 per cent where no mulch was used to 1.93 per cent in trees receiving a straw mulch In this orchard the mulching practice brought about a remarkable recovery of the original potassium-deficient trees in a period of one year. Kenworthy (1954) also determined the effect of sawdust, straw, and alfalfa mulches on the leaf potassium content of Montmorency cherries. He noted that straw and alfalfa were about equally effective in increasing the potassium content of cherry leaves and that the increase caused by the mulch was about 50 per cent. The use of mulches without a complete fertilizer resulted in a higher leaf potassium content than was obtained where such fertilizer was applied in the absence of a mulch.

The practice of mulching in nut and forest tree plantations is not common; consequently few data are available on the effect of organic residues on the absorption of potassium by these crops. However, Heiberg and White (1950) observed potassium starvation on a young coniferous plantation in a reforestation project in New York state. Their experiments using natural organic mulch materials such as logging debris and pine-hemlock humus resulted in marked increase in growth and vigor, and in color of needles. Chemical tests of needle tissue collected in the fall of several years showed a high correlation between potassium content and growth response. Needles from deficient trees were approximately 50 per cent lower in potassium than needles from healthy trees.

Hunter and Hammar (1952) found that over a five-year period the potassium content of pecan leaves was not significantly influenced by cultivation, mulching, or potash fertilization. It should be pointed out, however, that both mulched and cultivated plots had a cover crop of blue lupine each spring.

VIII. POTASSIUM IN PLANTS AS AFFECTED BY LEVEL OF VARIOUS NUTRIENTS

In order to critically evaluate the influence of soil fertility level on the absorption of potassium by crops, it is necessary to separate the interactive effects of potassium, phosphorus, nitrogen, calcium, and magnesium, and certain other nutrients. In many experiments this is not possible. Considerable data, however, are available which indicate that substantial changes in the levels of any of these nutrients may affect the potassium content of plants. Many workers have emphasized the importance of nutrient balance as it affects the chemical composition and growth of plants.

1. Soil Potassium Level

When the exchangeable potassium content of a soil is increased by the use of fertilizer, manure, mulch, or crop residue, the potassium content of crops is likewise increased. This statement is generally true, provided the level of soil potassium is not extremely high and the soil status of other cations and nitrogen and phosphorus is not markedly altered. In addition it must be assumed that soil moisture, aeration, and light do not limit plant growth.

Many investigators have reported increases in the potassium content of cereal straw, corn stover, legume and grass hay, vegetable and root crops, and foliage of fruit upon the application of potash fertilizer to soils. According to Snider (1947) the use of potassium on four Illinois soils relatively low in available potassium increased the potassium content of wheat and oat straw an average of 100 per cent. Drake *et al.* (1951) determined the composition of oat, barley, and wheat plants grown at eight different levels of exchangeable potassium. At the lowest level the per cent potassium was 0.13, 0.20, and 0.35, respectively, whereas at the highest level these values were 1.70, 1.71, and 1.57 per cent.

Lawton *et al.* (1952) found that the per cent potassium in legume-grass hay in 66 experiments was increased an average of 50 per cent by top-dressing 150 pounds of K_2O per acre on established stands. A similar increase in first-cutting alfalfa hay was noted by Snider (1947). In a greenhouse study Tucker and Smith (1952) noted that addition of potash fertilizer to soil always resulted in an increase in the potassium content of red clover. Bear and Prince (1945) reported excessive absorption of potassium by alfalfa and recommended application at frequent intervals during the life of alfalfa stands. The average increase in potassium content of grass hay grown at the Rothamsted Station during an 18-year period for PK — P and NPK — NP treatments was 1.45 and 1.60 per cent, respectively, according to Russell (1950).

In a comparison of potash and phosphate mixtures with phosphate alone Dunn and Rost (1948) showed that applied potash increased the potassium content of potato tops in 8 of 13 experiments located in the Red River Valley. Mehlich and Reed (1945) in studies with cotton found that at widely different levels of soil calcium, the potassium content of the cotton plants was increased as potash fertilizer applications were increased. Nelson *et al.* (1945) reported that use of increasing amounts of potash fertilizer greatly increased the potassium content of one variety of soybean seed but had little effect on two other varieties.

A number of experiments have been conducted evaluating the response of various vegetable crops to potash fertilizer and the differences in chemical composition due to treatment. Windham (1953) studied the effect of low and high levels of potassium applied to a sandy loam soil on 19 vegetable crops. When the analyses of plants grown at low and high levels were compared, the per cent potassium in spinach increased from 5.0 to 9.2, in table beets from 3.3 to 6.2, in celery from 2.1 to 5.0, and in cabbage from 2.8 to 4.6. In contrast, smaller changes in per cent potassium were noted in snap beans, sweet corn, lima beans, and garden peas.

Aldrich and Coony (1952) found that the potassium content of lemon leaves was significantly increased upon soil application of potash fertilizer. Boynton and Burrell (1944) also found that potash fertilization of McIntosh apple trees consistently raised the per cent potassium in the leaves.

2. *Nitrogen and Phosphorus*

Investigations of the effect of additions of phosphorus and nitrogen to crops on their absorption of potassium generally have indicated that a reduction often occurs, especially if the content of available soil potassium is limited. In most cases this decrease is the result of increased growth and dilution of the potassium within the plant. If the supply of available potassium is low, the use of phosphate or nitrogen fertilizers may even produce or intensify potassium deficiency symptoms. When phosphorus or nitrogen is a limiting factor in plant growth, the total potassium removed by crops is usually considerably higher when these nutrients and potassium are used together. For instance Lawton *et al.* (1952) found that the per cent potassium in legume hay was reduced from 1.52 to 1.35 when superphosphate was applied to soils already treated with potash. However, the total removal of potassium by first-cutting hay was 72 pounds on the phosphate plus potash areas and only 55 pounds on the potash plots.

On English soils that were deficient in potassium, Cowie (1942) noted that addition of both phosphorus and nitrogen enhanced potassium deficiency in potatoes. In another study with this same crop, Lorenz (1944) found that applications of nitrogen decreased the content of plant potassium.

Davidson (1949) concluded that the use of nitrogenous fertilizers on soils that were low in available potassium was likely to intensify deficiency symptoms of deciduous fruits. Reuther and Smith (1950) also noted that high applications of nitrogen reduced the potassium content of leaves of young orange trees. A similar trend in peach trees was reported by Havis and Gilkeson (1951). Cook (1950) has demonstrated in nutrient level experiments that the response of two flowering crops, calendula and forget-me-not, to potassium, is markedly different in the presence and absence of adequate nitrate and phosphorus levels.

3. Potassium–Sodium Relationship

The influence of sodium on the absorption of potassium by plants has been the subject of research for more than 50 years. Although sodium is not regarded as an essential element for plant growth, the yield response of certain crops to applications of sodium salt has suggested that sodium can substitute for potassium to a certain extent. This concept was developed by Wheeler and Tucker (1895) and others in studies of the fertilizer value of sodium salts. They showed that yield response of certain crops to sodium was obtained when available soil potassium was low. A short time later, Hartwell and Pember (1908), using culture solution methods, found that the addition of sodium in the presence of an optimum supply of potassium depressed the absorption of potassium and produced no additional growth.

More recent investigations indicate that the degree of response to sodium is dependent on the kind of crop, the amount of potassium available to the plant, and the quantity of sodium added. According to Harmer *et al.* (1953) the seasonal climate and extent of drainage may be important factors in the case of muck soils.

A large number of workers, including Osterhout (1912), Cooper and Wallace (1936), Collander (1941), Truog *et al.* (1953), and Harmer *et al.* (1953), have contributed information regarding the response of different crops to applied sodium. Larson and Pierre (1953) have suggested the following grouping: (1) crops that respond to sodium in the presence of an adequate supply of potassium; (2) crops that respond to sodium only where potassium is deficient, indicating that sodium partly replaces potassium in its function; (3) crops that respond very little or not at all to sodium under any conditions.

Plants which fall in the first group are members of the beet family, celery, swiss chard, turnips, and cabbages, radishes, and carrots to a lesser extent. Those crops in which sodium can partially substitute for potassium include barley, oats, wheat, rutabagas, cotton, tomatoes, broccoli, asparagus, alfalfa, and vetch. Some of the plants which show little or no response to sodium at any level of potassium are corn, lettuce, onions, peppermint, potatoes, soybeans, rye, and field beans.

Some variation exists in the literature regarding the degree of response of salt-responsive crops to sodium when no potassium is added as fertilizer. Harmer and Benne (1941) report that application of salt in the absence of potash produced low yields and marked potassium deficiency in these crops. On the other hand, Sayre and Vittum (1947) and Truog *et al.* (1953) report good yields of beets when little or no potash was used in their experiments. These differences can be explained on the basis that the muck soils with which Harmer and associates worked are extremely deficient in potassium, whereas the other experiments were conducted on mineral soils which contained reserves of available potassium. Holt and Volk (1945), working with sand cultures, found that sodium in the complete absence of potassium produced yields of sugar beets and turnips that were approximately 30 per cent of those obtained where both elements were present.

The effect of the addition of sodium on the potassium content of plants also seems to be dependent on several factors, namely, the nature of the crop and the supply of available potassium and sodium in the soil. For instance, little or no decrease in per cent potassium in plants was noted by Harmer and Benne (1941) when salt and potash fertilizer were applied to salt-responsive crops. In contrast, when the level of soil potassium was low, sodium depressed potassium absorption. Similar results were reported by Truog *et al.* (1953). On the other hand, Holt and Volk (1945) report that addition of sodium had little effect on the percentage of potassium in seven crops, when averaged as a group. Larson and Pierre (1953) report that addition of sodium to a soil will generally depress the uptake of potassium by plants. However, they pointed out that the result depended on the level of sodium and potassium available to the plant and the relative ease of plant absorption of these elements. When no potash was added to a Carrington loam soil, sodium did not affect the potassium content of table beets, oats, or corn. When appreciable potash was added, this same level of sodium depressed the potassium content of beets and oats but did not affect that of corn. Results on another soil indicate that the potassium content of all three crops was not affected by sodium when it was adequately fertilized with potash.

4. Potassium–Boron Relationship

The relationship between potassium and boron in plant nutrition has received much less attention than the more evident calcium–boron relationship. However, a number of workers have reported data which indicate that such a relationship exists. Saru (1938) observed that increased amounts of potash salts tended to reduce the occurrence of boron deficiency in sugar beets. In contrast it was noted by White-Stevens (1942) that when very high rates of potassium were added to boron-deficient soils, crops having high requirements for boron developed severe symptoms of boron deficiency. A similar trend was also found by Purvis and Hanna (1938) in their study of soils low in boron. In this work increased rates of applied potassium forced plant growth and intensified boron deficiency. Bear and Wallace (1949) grew Ranger alfalfa in sand cultures at various potassium and boron levels and found that plants grown in the presence of high potassium showed very severe boron deficiency symptoms, including a red pigmentation of terminal leaves. Plants grown in low potassium solutions exhibited a yellow mottling of the terminal leaves, which contained over twice as much boron as those from plants receiving the high amounts of potassium.

Minges *et al.* (1952) pointed out that "brown checking" of certain varieties of celery was due to continued use of large applications of potash fertilizer on soils relatively low in boron. K/B ratios in celery plants from clean fields averaged 2000/1, whereas for "brown checked" plants in affected fields this ratio rose to 3700/1.

Reeve and Shive (1944) found that the potassium concentration in sand cultures had a definite influence on the accumulation of boron in the tissues of corn and tomatoes. At any given level of boron in the substrate, there was a progressive increase in boron content of plants as the potassium concentration was raised. Where boron levels were high in sand cultures, extended symptoms of boron toxicity were accentuated by increased rates of applied potassium salts. However, at very low boron level, they found boron deficiency was accelerated when the potassium supply increased. Quantitative data to explain this anomaly were not available.

That the application of boron may increase the potassium content of plants has been noted by several workers. Parks *et al.* (1944) found this to be true with tomato leaflets. Smith and Reuther (1951) noted that when the boron supply was low in leaves of young orange trees, potassium accumulation was retarded.

5. *Potassium–Calcium Relationship*

Many workers have studied the effect of lime and magnesia on the absorption of potassium by plants. Considerable controversy regarding the influence of these materials in this respect is evident in the literature. Many of these conflicting data can be explained if the conditions under which the experiments were conducted are carefully evaluated. Reitemeier (1951) in a review of soil potassium has adequately discussed the effect of calcium on uptake of potassium by plants.

IX. ANALYSES FOR PLANT POTASSIUM

1. *Kind of Analysis*

Ash analysis has been used as a diagnostic technique to determine the nutritional status of plants and the fertilizer needs of soils since the early work of DeSaussure and Sprengel. Extensive use of this procedure has proved that the mineral composition of any crop is influenced by many factors, including species of plant, stage of maturity, anatomical structure and portion of the plant tested, as well as climate and soil conditions. Fundamental advances in quantitative studies of relationships between nutrients and crop yield have been made by Lagatu and Maume (1934), Wallace (1931), Thomas (1937), Chapman (1941), Lundegardh (1941), Shear *et al.* (1946), Tyner (1947), Goodall and Gregory (1947), and many others. In older methods of analysis, the quantities of minerals in the mature plant were determined, whereas under the newer concepts of foliar analysis, only the functionally assimilating leaves are analyzed.

More recently, analyses of green plant tissue have been successfully used to determine the concentrations of nutrients in many crop plants on a semiquantitative and quantitative basis. These procedures have been largely confined to tests for nitrogen, phosphorus, and potassium. A variety of methods of removing these nutrients from the plant tissue have been used, including chopping, freezing, macerating, and pressure extraction of plant sap. Consequently, the relative concentrations of potassium in the green tissue of poor and normal crops may vary considerably according to the method of analysis used. Among those who have used plant tissue tests as a diagnostic tool in the study of the potassium nutrition of plants are Hoffer (1926), Emmert (1934), Carolus (1938), Thornton *et al.* (1939), Hester (1941b), Scarseth (1943), and Cook *et al.* (1947).

2. *Critical Potassium Levels*

Interpretation of the relationship of foliar analyses to plant composition, growth and development, and applied nutrients has been approached in two ways, according to Thomas (1945). One criterion is the use of minimum values of nutrient composition below which an existing deficiency occurs. The second procedure involves evaluation of the interrelationships of nutrients as well as the use of the quantity factor in nutrition. Critical values may be set up on the basis of nutrient content or growth or on appearance of visual symptoms. A varied terminology has been used to characterize the areas of nutrient sufficiency and deficiency. Between these areas, minimum values should necessarily include a range of nutrient concentration but they are often considered at one level.

When plants or plant parts of similar age and variety and grown under similar cultural conditions were selected for comparison, many investigators found that critical levels of potassium in various plants could be established for both ash and fresh tissue analyses. For alfalfa and clover, the critical level is often considered to be about 1 per cent on the dry weight basis. This value also seems to be satisfactory for other legumes such as field beans or soybeans. McCollam (1952) has suggested that the minimum leaf potassium level for sugar beets falls between 1.0 and 1.5 per cent, whereas for barley it is between 0.5 and 1.0 per cent. For truck crops such as table beets, celery, lettuce, and tomatoes, the critical potassium content of the leaves is considered to lie between 0.75 and 1.50 per cent. For potatoes and tobacco the critical level is much higher.

Reuther and Boynton (1940) have suggested that a range of approximately 0.75 to 1.0 per cent potassium is intermediate between definite deficiency and sufficiency in apples, whereas a somewhat higher level of 1.0 to 1.5 per cent has been accepted by other workers for peaches. Chapman and Brown (1950) found no change in vegetative characteristics of citrus when the per cent of leaf potassium was above 0.35. However, an ample supply of this nutrient in some cases may mean values above 1.0 per cent.

Ulrich (1948) has presented the potassium content of leaves of various fruits associated with pronounced potassium deficiency as reported by many investigators. In most cases, these values fall between 0.2 and 0.6 per cent on a dry matter basis.

The range between sufficiency and deficiency for olive, almond, filbert, and walnut is somewhat lower than for most deciduous fruits, according to McCollam (1952).

3. *Part of Plant Tested*

As pointed out by Ulrich (1948) and others, all parts of a plant sampled from the same position of the plant structure do not necessarily contain the same concentration of potassium. For example the petioles of Ladino clover are more sensitive to changes in potassium than are the leaf blades. On this basis investigations have been carried out to determine which tissues of each crop plant are most suitable to use as criteria of its potassium requirements. Most evidence indicates that recently "matured" tissues are more satisfactory than immature, rapidly growing portions, than old tissues formed in early growth, or than fruit or seed.

Some workers conducting green tissue testing of agronomic plants have concluded that the stems and petioles are preferable for determining potassium levels, but others believe the leaf tissue better for diagnosing the requirements of certain plants for this nutrient. Cook and Millar (1953) consider the leaf petiole of such crops as sugar beets, field beans, soybeans, potatoes, and tomatoes as the best part of the plant to test for changing potassium concentrations. For small grains and alfalfa they suggest the use of stems, whereas for corn the leaf sheath has proved most useful. No qualification is given for most of these crops regarding the position of the plant part. Ohlrogge (1952) found the following plant parts most suitable for evaluating potassium in the plant tissue of various crops: soybeans—petioles; corn—blade tissue near the ear; small grain—leaf tissue near center of plant; alfalfa —upper third of stem and petiole. Kranz *et al.* (1948) report that for cotton either fine-cut petioles or leaf tissue was satisfactory, whereas for soybeans they felt the leaf tissue was most useful. According to Burkhart, and Page (1941) the lower blades of the peanut plant are most suitable for foliar diagnosis.

Brown (1943) suggested that the petiole of the first mature leaf of sugar beets was most satisfactory as a guide to the nutritional status of this plant.

Wallace (1951), using methods developed at the Long Ashton Experimental Station, has had most success in testing green leaf tissue for the purpose of relating the quantity of potassium in the green tissue of crops to their nutritional requirements. His recommendations are as follows: potatoes, tomatoes, and hops—leaves of comparable age from mid-stem position; onions—leaf bases; sugar beet and cauliflower—oldest upright leaf; cereals—internode adjacent to the growing point; and fruit trees—leaves from basal portions of well-exposed new leader growth.

Those workers interested in the nutrition of tree fruits have made significant studies of the various portions of the new growth to evaluate the potassium status of various orchard fruit. The large majority of these researches represent ash analyses, though some investigators such as Wallace (1951) and Daniel and Turk (1949) have successfully used green tissue tests to determine the concentration of potassium in certain tree fruits. An extensive list of the plant parts of various fruits which are commonly associated with pronounced deficiency symptoms has been presented by Ulrich (1948) and McCollam (1952). In most cases the current leaf tissue has been selected, but the position of the sampled leaves varied with different fruits and among workers reporting on the same fruit. In a recent survey of the nutritional conditions of Michigan orchards, Kenworthy (1953) selected leaves from the middle of the current season's growth for chemical analysis. Shear *et al.* (1946) conclude that leaf composition is the only valid criterion of the nutritional status of plants, since it represents a measure of all the environmental factors which have influenced nutrient accumulation. Accordingly, they felt it essential that leaf samples be taken from nodal shoots and the same position on shoots and at a time of sampling when all shoots are as nearly as possible at the same stage of physical development.

On the other hand, Ramig and Vandecaveye (1950) working with raspberries in nutrient cultures, found that leaf petioles were more useful than leaf blades in determining the potassium status of plants.

With some crops it is necessary to change the plant part to be tested as the plant matures. A good example is corn, in which the whole stalk may be used in early growth, whereas in a more mature state the leaf blades near the ear are more commonly selected. In certain cases, it is desirable, according to Cook and Millar (1953), to test both the old and new tissues to obtain a more accurate picture of the concentration of potassium within the entire plant. Drake and Scarseth (1939) found that the bottom leaves of tobacco plants grown under glass were lower in potassium than top leaves when only small amounts of potash fertilizer were added to the soil. At high fertilizer rates, the reverse condition was apparent. Ulrich (1948) also noted a similar trend in tomatoes in the vegetative stage which received widely varying amounts of applied potassium.

4. *Time of Sampling and Testing*

The time of sampling for potassium analyses of plants to determine critical concentrations during growth depends largely on the type of crop, the potassium status of the soil, and the purpose of the study. Since, in early growth of many annual crops, this nutrient is usually accumulated at a faster rate than it is utilized, neither ash analyses nor plant tissue tests in this period are likely to indicate the potassium requirements in the latter part of the growing season. Factors such as the rate of plant growth, the ability of the soil to release nonexchangeable potassium, and the concentration of other cations in the soil are important in determining when a critical level of potassium may exist in crops. Though deficiency symptoms may occur in the early season, they are more likely to show as flowering is approached. According to Loehwing (1951), in this catabolic stage of plant development a general internal redistribution of nutrients is initiated and continues into the bloom stage. Kranz *et al.* (1948) found the most critical stage of growth for tissue tests for corn was from silking through early ear formation, whereas for soybeans and cotton, potassium tests in the full bloom proved most desirable. Tests made later were complicated by fruiting and leaf maturity and deterioration.

It is sometimes advantageous to sample at intervals of two to three weeks with fast-growing crops, but in the case of crops like carrots and sugar beets, tests for potassium later in the growing season may indicate a critical need for added potassium. Hester (1948) has found that carrots absorb only 4 per cent of their total potassium requirement in the first 70 days after seeding, 27 per cent in the next 30 days, and 69 per cent in the following 30 days. Garden peas, on the other hand, remove enough potassium in the first month after planting to satisfy 5 per cent of their total needs, 55 per cent in the following month, and 40 per cent in the final two weeks before harvest.

When single samples are collected to diagnose the nutritional status of a crop, the selection of time probably coincides with the later part of the grand period of growth. Ulrich (1948) reported that the midpoint of berry development was a desirable time for grapes. Lilleland (1946) suggested that for deciduous fruits in California the middle of June to the middle of August was a satisfactory sampling period. Lawton *et al.* (1952) obtained good correlation between deficiency symptoms and potassium analyses of alfalfa at about the quarter-bloom stage.

REFERENCES

Aldrich, D. G., and Coony, J. J. 1952. *Proc. Am. Soc. Hort. Sci.* **59**, 13–21.

Anderson, P. J., Swanback, T. R., and Street, O. E. 1939. *Connecticut Agr. Expt. Sta. Bull.* **422**.

Arnon, D. I., and Hoagland, D. R. 1940. *Soil Sci.* **50**, 463–486.

Arnon, D. I., and Hoagland, D. R. 1943. *Botan. Gaz.* **104**, 576–590.

Baker, C. E. 1948. *Proc. Am. Soc. Hort. Sci.* **51**, 205–208.

Bartholomew, R. P., and Janssen, G. 1929. *J. Am. Soc. Agron.* **21**, 751–765.

Batjer, L. P., and Magness, J. R. 1938. *Proc. Am. Soc. Hort. Sci.* **36**, 197–201.

Bear, F. E., and Prince, A. J. 1945. *J. Am. Soc. Agron.* **37**, 217–222.

Bear, F. E., and Wallace, A. 1949. *Plant Physiol.* **24**, 664–680.

Beeson, K. C. 1941. *U. S. Dept. Agr. Misc. Publ.* **369**.

Blaser, R. E., and Brady, N. C. 1950. *Agron. J.* **42**, 128–135.

Boller, C. A., and Stephenson, R. E. 1948. *Proc. Am. Soc. Hort. Sci.* **48**, 37–39.

Borden, R. J. 1936. *Hawaiian Planters' Record* **40**, 143–156.

Bower, C. A., Browning, G. A., and Norton, R. A. 1944. *Soil Sci. Soc. Amer., Proc.* **9**, 142–146.

Boyer, P. D., Lardy, H. A., and Phillips, P. H. 1943. *J. Biol. Chem.* **149**, 529–541.

Boynton, D., and Burrell, A. B. 1944. *Soil Sci.* **58**, 441–454.

Boynton, D., and Compton, O. C. 1945. *Soil Sci.* **59**, 339–352.

Breazale, J. F. 1930. *Arizona Agr. Expt. Sta. Tech. Bull.* **29**, 137–177.

Brown, R. J. 1943. *Soil Sci.* **56**, 213–222.

Brown, R. T., and Potter, G. F. 1949. *Proc. Am. Soc. Hort. Sci.* **54**, 53–56.

Browne, C. A. 1938. "Soils and Men," U. S. Dept. Agr. Yearbook, pp. 777–806. U. S. Government Printing Office, Washington, D. C.

Broyer, T. C. 1951. *In* "Mineral Nutrition of Plants," pp. 187–250. E. Truog, ed. University of Wisconsin Press, Madison, Wisconsin.

Bruno, A. 1928. *Rev. viticult.* **69,** 60–62.

Buckner, G. D. 1915. *J. Agr. Research* **5,** 449–459.

Burd, J. S. 1919. *J. Agr. Research* **18,** 51–72.

Burkhart, L., and Page, N. R. 1941. *J. Am. Soc. Agron.* **33,** 743–755.

Carolus, R. L. 1936. *Am. Potato J.* **14,** 141–153.

Carolus, R. L. 1938. *Virginia Truck Expt. Sta. Bull.* **98,** 1531–1556.

Chang, H. T., and Loomis, W. E. 1945. *Plant Physiol.* **20,** 221–232.

Chapman, G. W. 1941. *Soil Sci.* **52,** 63–81.

Chapman, H. D., and Brown, S. M. 1950. *Hilgardia* **19,** 501–540.

Chapman, H. D., Brown, S. M., and Rayner, D. S. 1947. *Hilgardia* **17,** 619–650.

Collander, R. 1941. *Plant Physiol.* **16,** 691–720.

Cook, R. L., Robertson, L. S., Lawton, K., and Rood, P. J. 1947. *Soil Sci. Soc. Amer., Proc.* **12,** 379–381.

Cook, R. L. 1950. *Proc. Am. Soc. Hort. Sci.* **56,** 446–456.

Cook, R. L., and Millar, C. E. 1953. *Michigan Agr. Expt. Sta. Spec. Bull.* **353.**

Cooper, H. P., and Wallace, R. W. 1936. *South Carolina Agr. Expt. Sta. Ann. Rept.* **49,** 109–115.

Cooper, H. P., Mitchell, J. H., and Page, N. R. 1947. *Soil Sci. Soc. Amer., Proc.* **12,** 364–369.

Cowie, G. A. 1942. *Ann. Appl. Biol.* **29,** 333–340.

Daniel, W. H., and Turk, L. M. 1949. *Michigan Agr. Expt. Sta. Quart. Bull.* **32** (2), 199–205.

Davidson, J. 1926. *J. Am. Soc. Agron.* **18,** 962–967.

Davidson, O. W. 1949. *In* "Hunger Signs in Crops," 2nd ed., pp. 191–237. The American Society of Agronomy and the National Fertilizer Association, Washington, D. C.

Deleono, N. T. 1932. *Biol. d. Pflanz.* **19,** 249–265.

Dowding, E. S. 1925. *Ann. Botany (London)* **39,** 459–474.

Drake, M., and Scarseth, G. D. 1939. *Soil Sci. Soc. Amer., Proc.* **4,** 201–204.

Drake, M., Colby, W. G., and Vengris, J. 1951. *Soil Sci.* **72,** 139–147.

Drosdoff, M., Sell, H. M., and Gilbert, S. G. 1947. *Plant Physiol.* **22,** 538–547.

Dunn, L. E., and Rost, C. O. 1948. *Soil Sci. Soc. Amer., Proc.* **13,** 374–379.

Eaton, F. M., and Joham, H. E. 1944. *Plant Physiol.* **19,** 507–518.

Eckart, C. F. 1905. *Hawaiin Planters' Monthly* **24,** 344–364.

Eckstein, O., Bruno, A., and Turrentine, J. W. 1937. "Potash Deficiency Symptoms." Westermann and Co., New York.

Emmert, E. M. 1934. *Kentucky Agr. Expt. Sta. Circ.* **43.**

Emmert, E. M. 1936. *Soil Science* **41,** 67–70.

Elgabaly, M. M., and Wiklander, L. 1949. *Ann. Agr. Coll. Sweden* **16,** 334.

Fonder, J. F. 1929. *J. Am. Soc. Agron.* **21,** 732–750.

Gericke, W. F. 1925. *Botan. Gaz.* **80,** 410–425.

Gile, P. L., and Carrero, J. O. 1915. *J. Agr. Research* **5,** 357–364.

Goodall, D. W., and Gregory, F. G. 1947. *Imp. Bur. Hort. and Plantation Crops, East Malling, Kent, Tech. Commun.* **17,** 1–167.

Gourley, J. H. 1941. *Am. Pomol. Soc., Proc. 56th Convention,* pp. 53–64.

Gregory, F. G. 1937. *Ann. Rev. Biochem.* **6,** 577–578.

Gregory, F. G., and Crowther, F. 1931. *Ann. Botany* (*London*) **45**, 579–592.

Gregory, F. G., and Sen, P. K. 1937. *Ann. Botany* (*London*) **50**, 521–561.

Grizzard, A. L., Davies, H. R., and Kangas, L. R. 1942. *J. Am. Soc. Agron.* **34**, 327–339.

Haley, D. E., and Reid, J. J. 1943. *Soil Sci.* **55**, 79–86.

Hall, W. C. 1949. *Plant Physiol.* **24**, 755–769.

Harley, C. P., Moon, H. H., and Regeimbal, L. O. 1951. *Proc. Am. Soc. Hort. Sci.* **57**, 17–23.

Harmer, P. M., and Benne, E. J. 1941. *J. Am. Soc. Agron.* **33**, 952–979.

Harmer, P. M., Benne, E. J., Laughlin, W., and Key, C. 1953. *Soil Sci.* **76**, 1–18.

Hartt, C. E. 1934. *Plant Physiol.* **9**, 452–490.

Hartwell, B. L., and Pember, F. R. 1908. *Rhode Island Agr. Expt. Sta. Rept.* **1908**, 243-285.

Harvey, R. B. 1942. Minnesota University Farm Mimeo. Progress Rept., pp. 2, March 31st.

Havis, L., and Gilkeson, A. L. 1951. *Proc. Am. Soc. Hort. Sci.* **57**, 24–30.

Heiberg, S. O., and White, D. P. 1950. *Soil Sci. Soc. Amer., Proc.* **15**, 369–376.

Hellriegel, F. H. 1898. *Arb. Deut. Landw. Gesell.* **34**, 1.

Hester, J. B. 1941a. *Soil Sci. Soc. Amer., Proc.* **6**, 243–245.

Hester, J. B. 1941b. *Com. Fertilizer Yearbook* **1941**, 31–39.

Hester, J. B. 1948. "Diagnostic Techniques in Soils and Crops," pp. 105–136. American Potash Institute, Washington, D. C.

Hibbard, R. P., and Grigsby, B. H. 1934. *Michigan Agr. Expt. Sta. Tech. Bull.* **141.**

Hoagland, D. R. 1944. "Lectures on the Inorganic Nutrition of Plants." Chronica Botanica Co., Waltham, Massachusetts.

Hoagland, D. R., and Broyer, T. C. 1936. *Plant Physiol.* **11**, 471–507.

Hoffer, G. N. 1926. *Indiana Agr. Expt. Sta. Bull.* **298**, 1–31.

Hoffer, G. N. 1938. *Ind. Eng. Chem.* **30**, 885–889.

Hoffer, G. N. 1945. *Better Crops with Plant Food* **29** (1), 6.

Hoffer, G. N., and Krantz, B. A. 1949. *In* "Hunger Signs in Crops," 2nd ed., pp. 59–84. The American Society of Agronomy and the National Fertilizer Association, Washington, D. C.

Holt, M. E., and Volk, N. J. 1945. *J. Am. Soc. Agron.* **37**, 821–827.

Hopkins, H. T., Specht, A. W., and Hendricks, S. B. 1950. *Plant Physiol.* **25**, 193–209.

Hunter, J. H., and Hammar, H. E. 1952. *Soil Sci. Soc. Amer., Proc.* **16**, 346–349.

Jackson, M. L., Evans, C. E., Attoe, O. J., Huber, J. L., and Kaudy, J. C. 1947. *Soil Sci. Soc. Amer., Proc.* **12**, 282–288.

Jacobson, L., Overstreet, R., King, H. M., and Handley, R. 1950. *Plant Physiol.* **25**, 639–647.

James, W. O., and Penston, N. L. 1933. *Ann. Botany* (*London*) **47**, 279–293.

Jenny, H., Overstreet, R., and Ayers, A. 1939. *Soil Sci.* **48**, 9–24.

Jenny, H., and Overstreet, R. 1939. *Soil Sci.* **47**, 257–272.

Kenworthy, A. L. 1953. *Michigan Agr. Expt. Sta. Tech. Bull.* **237.**

Kenworthy, A. L. 1954. *Michigan Agr. Expt. Sta. Tech. Bull.* **243.**

Knowles, F., and Watkins, J. E. 1931. *J. Agr. Sci.* **21**, 612–637.

Krantz, B. A., Nelson, W. L., and Burkhart, L. F. 1948. *In* "Diagnostic Techniques for Soils and Crops," pp. 137–156. American Potash Institute, Washington, D. C.

Lagatu, H., and Maume, L. 1934. *Ann. école natl. agr. Montpellier* **22**, 257–306.

Larson, W. E., and Pierre, W. H. 1953. *Soil Sci.* **76**, 51–64.

Laughlin, W. 1947. M.S. Thesis, Michigan State College, East Lansing, Michigan.

Lawton, K. 1945a. *Soil Sci. Soc. Amer., Proc.* **10,** 263–268.

Lawton, K. 1945b. *Iowa Agr. Expt. Sta. Ann. Rept.* 1945, pp. 129–132.

Lawton, K., and Browning, G. A. 1948. *Soil Sci. Soc. Amer., Proc.* **13,** 311–317.

Lawton, K., Robertson, L. S., Cook, R. L., and Rood, P. J. 1952. *Michigan Agr. Expt. Sta. Quart. Bull.* **34** (4), 466–471.

Le Clerc, J. A., and Yoder, P. A. 1912. *8th Intern. Congr. Appl. Chem. Orig. Commun.* **26,** 137–150.

Lemon, E. R., and Erickson, A. E. 1952. *Soil Sci. Soc. Amer., Proc.* **16,** 160–163.

Lewis, C. L., and Eisenmenger, W. S. 1948. *Soil Sci.* **65,** 495–500.

Lilleland, O. 1946. *The Blue Anchor* **23** (No. 1). February.

Loehwing, W. F. 1951. *In* "Mineral Nutrition of Plants," pp. 343–358. E. Troug, ed. University of Wisconsin Press, Madison, Wisconsin.

Loew, O. 1934. *Ernähr. Pflanze* **30,** 141–144.

Lorenz, O. A. 1944. *Am. Potato J.* **21,** 179–191.

Loustalot, A. J. 1949. *Proc. Am. Soc. Hort. Sci.* **53,** 517–519.

Loustalot, A. J., Gilbert, S. G., and Drosdoff, M. 1950. *Plant Physiol.* **25,** 394–412.

Lucas, R. E., Scarseth, G. D., and Sieling, D. H. 1942. *Purdue Agr. Expt. Sta. Bull.* **468.**

Lundegardh, H. 1932. "Die Nabrstoffaufnahme." Gustav. Fisher, Jena.

Lundegardh, H. 1940. *Ann. Agr. Coll. Sweden* **8,** 234–404.

Lundegardh, H. 1941. *Ann. landwirtsch. Hochschule Schwed.* **9,** 127–221.

Mach, F., and Hermann, R. 1934. *Landwirtsch. Vers. Sta.* **119,** 1–173.

Martin, J. C., Overstreet, R., and Hoagland, D. R. 1945. *Soil Sci. Soc. Amer., Proc.* **10,** 94–101.

Mason, T. G., and Maskell, E. J. 1931. *Ann. Botany (London)* **45,** 125–170.

Mattson, S. 1948. *Ann. Agr. Coll. Sweden* **15,** 308.

McCollam, M. E. 1952. *Better Crops with Plant Food* **36** (10), 6.

McMurtrey, J. E. 1948. *In* "Diagnostic Techniques for Soils and Crops," pp. 231–290. American Potash Institute, Washington, D. C.

McMurtrey, J. E. and others. 1949. "Hunger Signs in Crops," 2nd ed. The American Society of Agronomy and the National Fertilizer Association, Washington, D. C.

Mehlich, A., and Reed, J. F. 1945. *Soil Sci. Soc. Amer., Proc.* **10,** 87–93.

Miller, E. C. 1938. "Plant Physiology." McGraw-Hill Book Company, New York.

Minges, P. A., Yamaguchi, M., Knott, J. E., Spurr, A. R., and Welch, J. E. 1952. *Calif. Agr.* **6** (12), 5–6.

Moody, J. E., Lillard, J. H., and Edminster, T. W. 1952. *Soil Sci. Soc. Amer., Proc.* **16,** 190–194.

Morrison, F. B. 1949. "Feeds and Feeding," 21st. ed. The Morrison Publishing Co., Ithaca, New York.

Mulder, E. C. 1949. *Plant and Soil* **2,** 50–121.

Nelson, W. L. 1949. *Agron. J.* **41,** 101–103.

Nelson, W. L., Burkhart, L., and Colwell, W. L. 1945. *Soil Sci. Soc. Amer., Proc.* **10,** 224–229.

Newton, J. D. 1928. *Soil Sci.* **26,** 85–91.

Nightingale, G. T. 1942. *Botan. Gaz.* **103,** 409–456.

Nightingale, G. T. 1943. *Soil Sci.* **55,** 73–78.

Nightingale, G. T., Schermerhorn, L. G., and Robbins, W. R. 1930. *New Jersey Agr. Expt. Sta. Bull.* **449.**

Ohlrogge, A. J. 1952. *Purdue Agr. Expt. Sta. Bull.* **584.**

Osterhout, W. J. V. 1912. *Botan. Gaz.* **54**, 532–536.

Overstreet, R., Jacobson, L., and Handley, R. 1952. *Plant Physiol.* **27**, 583–590.

Page, J. B., Willard, C. J., and McCuen, G. W. 1946. *Soil Sci. Soc. Amer., Proc.* **11**, 77–80.

Page, J. B., and Bodman, G. B. 1951. *In* "Mineral Nutrition of Plants," pp. 133–166. E. Troug, ed. University of Wisconsin Press, Madison, Wisconsin.

Parks, R. Q., Lyon, C. B., and Hood, S. L. 1944. *Plant Physiol.* **19**, 404–419.

Pepkowitz, L., and Shive, J. W. 1944. *Soil Sci.* **57**, 143–154.

Prince, F. S., Blood, P. T., Percival, C. P., and Scripture, P. N. 1942. *New Hampshire Agr. Expt. Sta. Circ.* **58**.

Purvis, E. R., and Hanna, W. J. 1938. *Soil Sci. Soc. Amer., Proc.* **3**, 205–209.

Ramig, R. E., and Vandecaveye, S. C. 1950. *Plant Physiol.* **25**, 617–629.

Reeve, E., and Shive, J. W. 1944. *Soil Sci.* **57**, 1–13.

Reitemeier, R. F. 1951. *Advances in Agron.* **3**, 113–159.

Remy, T., and Liesegang, H. 1926. *Landwirtsch. Jahrb.* **64**, 213–221.

Reuther, W., and Boynton, D. 1940. *Proc. Am. Soc. Hort. Sci.* **37**, 32–38.

Reuther, W., and Smith, P. F. 1950. *Proc. Am. Soc. Hort. Sci.* **56**, 27–33.

Reuther, W., and Smith, P. F. 1952. *Proc. Am. Soc. Hort. Sci.* **59**, 1–12.

Rich, A. E., and Odland, T. E. 1947. *J. Am. Soc. Agron.* **39**, 390–394.

Richards, F. J., and Templeman, W. G. 1936. *Ann. Botany (London)* **50**, 367–401.

Richards, L. A., and Wadleigh, C. H. 1952. *In* "Soil Physical Conditions and Plant Growth," pp. 73–225. Academic Press, New York.

Romaine, J. D. 1940. *Better Crops with Plant Food* **24** (3), 6.

Russell, E. J. 1950. "Soil Conditions and Plant Growth," 8th ed. Longmans, Green and Company, New York.

Saru, N. 1938. *Kühn.-Arch.* **48**, 1–51.

Sayre, C. B., and Vittum, M. T. 1947. *J. Am. Soc. Agron.* **39**, 153–161.

Scarseth, G. D. 1943. *Soil Sci.* **55**, 113–120.

Shear, C. B., Crane, H. L., and Myers, A. T. 1946. *Proc. Am. Soc. Hort. Sci.* **47**, 239–248.

Shive, J. W., and Robbins, W. R. 1939. *Ann. Rev. Biochem.* **8**, 503–520.

Singh, B. N., and Singh, L. B. 1939. *Soil Sci.* **47**, 227–235.

Skinner, J. J., and Purvis, E. R. 1949. *In* "Hunger Signs in Crops," 2nd ed. pp. 117–214. The American Society of Agronomy and the National Fertilizer Association, Washington, D. C.

Smith, P. F., and Reuther, W. 1949. *Plant Physiol.* **24**, 455–461.

Smith, P. F., and Reuther, W. 1950. *Proc. Am. Soc. Hort. Sci.* **55**, 61–72.

Smith, P. F., and Reuther, W. 1951. *Plant Physiol.* **26**, 110–114.

Snider, H. J. 1947. *Better Crops with Plant Food* **31** (5), 19.

Sommer, A. L. 1941. *Ann. Rev. Biochem.* **10**, 471–490.

Sprague, M. A., and Eby, C. 1948. *New Jersey Agr. Expt. Sta. Bull.* **736**.

Steinberg, R. A. 1947. *J. Agr. Research* **75**, 81–92.

Steinberg, R. A. 1951. *In* "Mineral Nutrition of Plants," pp. 359–388. E. Truog, ed. University of Wisconsin Press, Madison, Wisconsin.

Steward, F. C., Berry, W. E., and Broyer, T. C. 1936. *Ann. Botany (London)* **50**, 1–22.

Stoklasa, J. 1934. *Ernähr. Pflanze* **30**, 299–307.

Stoklasa, J. 1936. *Ernähr Pflanze* **32**, 27–31.

Stubblefield, F. M., and DeTurk, E. E. 1940. *Soil Sci. Soc. Amer., Proc.* **5**, 120–124.

T'Hart, M. L. 1949. *Plant and Soil* **1**, 264–270.

Thomas, W. 1937. *Plant Physiol.* **12,** 571–599.

Thomas, W. 1945. *Soil Sci.* **59,** 353–374.

Thomas, W., and Mack, W. B. 1941. *Science* **93,** 188–189.

Thornton, S. F., Connor, S. D., and Fraser, R. R. 1939. *Purdue Agr. Expt. Sta. Circ.* **204.**

Tisdale, H. B., and Dick, J. B. 1942. *J. Am. Soc. Agron.* **34,** 405–426.

Truog, E., Berger, K. C., and Attoe, O. J. 1953. *Soil Sci.* **76,** 41–50.

Tucker, T. C., and Smith, F. W. 1952. *Soil Sci. Soc. Amer., Proc.* **16,** 252–255.

Turtschin, T. W. 1934. *Z. Pflanzenernähr., Düng. u. Bodenk.* **35A,** 343–347.

Tyner, E. H. 1947. *Soil Sci. Soc. Amer., Proc.* **11,** 317–327.

Tyson, J., and Crabb, G. A., Jr. 1952. *Michigan. Agr. Expt. Sta. Quart. Bull.* **34** (4), 412–424.

Ulrich, A. 1948. *In* "Diagnostic Techniques for Soils and Crops," pp. 157–198. H. B. Kitchen, ed. American Potash Institute, Washington, D. C.

Van Slyke, L. L. 1932. "Fertilizers and Crop Production." Orange Judd Publishing Company, New York.

Vengris, J., Drake, M., Colby, W. G., and Bart, J. 1953. *Agron. J.* **45,** 213–218.

Vlamis, J., and Davis, A. R. 1944. *Plant Physiol.* **19,** 33–51.

Vladimirov, A. V. 1945. *Soil Sci.* **60,** 377–385.

Volk, G. W. 1947. *J. Am. Soc. Agron.* **39,** 93–106.

Volk, N. J. 1934. *Soil Sci.* **37,** 267–287.

Wadleigh, C. H., and Richards, L. A. 1951. *In* "Mineral Nutrition of Plants," pp. 411–450. E. Truog, ed. University of Wisconsin Press, Madison, Wisconsin.

Wall, M. E. 1939. *Soil Sci.* **47,** 143–161.

Wall, M. E. 1940. *Soil Sci.* **49,** 393–407.

Wallace, T. 1931. *J. Pomol. and Hort. Sci.* **9,** 111–121.

Wallace, T., 1951. "The Diagnosis of Mineral Deficiencies in Plants." His Majesty's Stationery Office, London.

Warburg, O. 1919. *Biochem. Z.* **100,** 230.

Watson, A. 1949. Ph.D. Thesis, Michigan State College, East Lansing, Michigan.

Watson, J. D. 1947. *Ann. Botany (London)* **11,** 375–407.

Wheeler, H. J., and Tucker, G. M. 1895. *Rhode Island Agr. Expt. Sta. Ann. Rept.* **1895,** 215–231.

White-Stevens, R. H. 1942. *Better Crops with Plant Food* **26** (2), 6.

Wilfarth, H., and Wimmer, G. 1902. *Arb. Deut. Landw. Gessell* **68,** 246–272.

Williams, D. E., and Coleman, N. T. 1950. *Plant and Soil* **2,** 243.

Windham, S. 1953. Ph.D. Thesis, Michigan State College, East Lansing, Michigan.

Woodford, E. K., and McCalla, A. G. 1936. *Can. J. Research* **14C,** 245–266.

Sorghum Improvement

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I. INTRODUCTION

Changes in the production of sorghum during the past 15 years have been fully as striking as those of any other crop of major importance in the United States. These changes were brought about by typical American farmers who adopted the improvements developed by state, federal, private, and commercial workers. Grain sorghum, formerly a feed crop for local use, is now also a cash crop for industrial use and foreign export. The chief change in sorghum on the farm has been a 2-ft. reduction in the height of the stalks. This has made combine harvesting of grain sorghum almost universal, whereas formerly it was scarcely feasible. Other changes include: (1) expanded production into northern and high-altitude sections having a short growing season, (2) industrial uses of sorghum, (3) new disease-resistant varieties, (4) forage sorghums having palatable seed, (5) forage sorghums low in prussic acid, (6) artificial drying of grain sorghum at country points, and (7) growing of grain sorghum in close rows.

The extensive sorghum accomplishments listed above were put into practice without the aid of any special promotional organization. The small group of sorghum research workers operated with a minimum of high-level planning. They conducted a minimum of rigid uniform regional yield trials. Breeding plans were kept flexible to avoid stagnation resulting from conformity to prevalent beliefs. The individual approach to breeding objectives was encouraged to avoid disaster from diseases that often build up rapidly on widely grown varieties evolved from a narrow gene base. Materials and ideas were interchanged freely among the workers and promising strains were tested at many stations. Varieties bred in one state often were first released in some other state because they appeared to be more valuable there.

During the past decade, sorghum has been grown annually on approximately 16 million acres in the United States. Of this acreage about 42 per cent was harvested for grain, 50 per cent for forage, 5 per cent for silage, 1 per cent for syrup, and 2 per cent for broomcorn. In the most recent years, the acreage harvested for grain has exceeded that harvested for forage. In addition to the sorghum acreage, Sudan grass is grown on approximately 3 million acres, of which the largest part is grazed and the rest cut for hay or plowed under for green manure. Sorghum occupies an acreage in the United States above that of barley and below that of cotton. Production is concentrated in the Great Plains from Texas to South Dakota and in the irrigated valleys of the Southwest. In those areas sorghum is a major crop.

II. Recent Developments in Sorghum

1. *Development of Combine Grain Sorghum*

The grain sorghum varieties grown before 1928 were from 4½ to 6 ft. in height, and some of them bore recurved heads or had weak stalks. They were poorly suited to harvesting with a combine and thus were mostly headed by hand. At a meeting of sorghum workers at Manhattan, Kansas, in the spring of 1926, the desirability of a new machine to harvest grain sorghum was discussed. An agricultural engineer present suggested that it would be much easier for the breeders to develop the crop to fit existing machines. This possibility had been anticipated and erect, short-stalked strains already were in plot tests. Certain selections made from F_2 generation Kafir-Milo crosses in 1920, and thereafter, had short stalks, erect heads, and Milo-like grains. Some of these were backcrossed to Milo, and selected progenies from these also were tested. One of these, named BEAVER, was distributed in Oklahoma in 1928 (Martin, 1951). A selection from the original cross, named WHEATLAND, was distributed in Kansas and Oklahoma about two years later. Both BEAVER and WHEATLAND were bred by J. B. Sieglinger at Woodward, Oklahoma. These short, erect varieties could be combined successfully. Their acreage increased gradually up to 1940.

Combine grain sorghum leaped into importance after the release of the MARTIN variety in 1941, followed by PLAINSMAN, WESTLAND, CAPROCK, and MIDLAND shortly thereafter. These, together with COMBINE 7078, EARLY HEGARI, COMBINE KAFIR 44-14, and REDBINE 60, are the leading varieties at the present time. By 1953, about 98 per cent of the sorghum harvested for grain consisted of combine types. The 32 varieties that have become established on farms since 1928 are listed in Table I. Five of the varieties listed were selected by farmers and the remainder by six state agricultural experiment stations and the United States Department of Agriculture. At least four other varieties that were released did not become established.

Of the five varieties developed by farmers, MARTIN and BLANKENSHIP were selected from WHEATLAND, EDWARDS was selected from PLAINSMAN, and WHITE MARTIN was selected from MARTIN. EARLY HEGARI was selected from DWARF HEGARI on a farm near Otis, Colorado, and was grown on a few neighboring farms. Later it was released in Texas after experimental trials proved its value. Nearly all of the varieties listed in Table I were introduced to other states shortly after their release, through either commercial or official channels.

The labor for combining grain sorghum is about one-eighth that required by the old methods of hand heading before threshing (Fig. 1). The reduced labor for harvesting combine varieties has resulted in expanded production of some 20 million bu. annually as compared with production before 1940. The shortage of labor during and since World War II would have precluded the harvesting of even a normal prewar acreage of the older varieties. The saving in harvesting cost amounting to 4 dollars or more an acre during recent years totals some 30 to

TABLE I

Combine Grain Sorghums Widely Adopted since 1928

Variety	Where bred	Where first released
BEAVER	Oklahoma	Oklahoma
WHEATLAND	Oklahoma	Kansas, Oklahoma
COLBY	Oklahoma	Kansas
DAY	Oklahoma	Nebraska
COES	Colorado	Colorado
DOUBLE DWARF MILO 38	California	California
MARTIN*	Texas	Texas
PLAINSMAN	Texas	Texas
CAPROCK	Texas	Texas
EARLY HEGARI*	Colorado	Texas
WESTLAND	Kansas	Kansas
MIDLAND	Kansas	Kansas
CODY	Kansas	Kansas, Texas
BONITA	Texas	Texas
RESISTANT WHEATLAND 288	Kansas	Oklahoma
COMBINE KAFIR 24-43	Oklahoma	Texas
COMBINE KAFIR 44-14	Oklahoma	Oklahoma
REDBINE 60	Texas	Texas
REDBINE 66	Texas	Texas
COMBINE KAFIR 60	Texas	Texas, Nebraska
COMBINE 7078	Texas	Texas
NORGHUM	South Dakota	South Dakota
REDLAN	Oklahoma	Oklahoma
RELIANCE	South Dakota	South Dakota
DARSET	Oklahoma	Oklahoma
MILOCA	Texas	Texas
DOUBLE DWARF YELLOW SOONER MILO	Texas	Texas
DOUBLE DWARF WHITE SOONER MILO	Texas	Texas
GURNO	Kansas	Colorado
BLANKENSHIP*	Kansas	Kansas
EDWARDS*	Texas	Texas
WHITE MARTIN*	Kansas	Kansas

* Selected by a farmer.

50 million dollars a year. The shipping of grain sorghum to other countries for food, the establishment of a sorghum starch industry, and the feeding of the large livestock population would scarcely have been possible without the development of combine grain sorghum.

A root and stalk rot, the so-called Milo disease caused by the fungus *Periconia circinata*, was first observed in experimental plots at Garden City, Kansas, in 1925. Two years later it destroyed the crop of DWARF YELLOW MILO on several irrigated fertilizer plots at Garden City. Two healthy plants survived, and the seed was planted in the infested soil in

1928. One plant segregated, showing it to be a natural hybrid. The other progeny bred true for resistance and other characters. This selection, named FINNEY, was first released in New Mexico, and later in Texas and Kansas.

Numerous tests on infested soil at Garden City showed that the disease attacked only varieties of Milo, certain Milo derivatives, and an occasional variety, possibly of Milo extraction, such as DARSO and EXTRA EARLY SUMAC. This made it possible to breed resistant strains readily, particularly since resistance was controlled by a single gene. Also, subsequent tests showed that all susceptible varieties produced occasional healthy mutant plants that were evident in infested soil in the field or in greenhouse flats. Some of the mutants bred true for resistance, but others segregated. Resistant mutants occurred in ratios of from 1/200 to 1/2000 in susceptible varieties. TEXAS MILO was selected from an infested field in Texas, and DOUBLE DWARF 38 was selected from a field of DOUBLE DWARF MILO in California. These two strains were chosen for increase from among many other resistant lines that were tested on infested soil. WESTLAND and RESISTANT WHEATLAND were se-

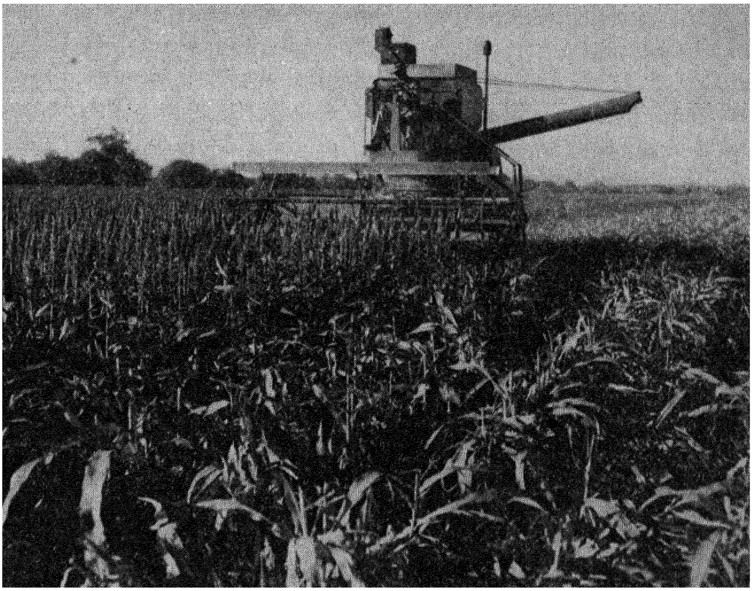

FIG. 1. A field of MARTIN being harvested for seed in the Salt River Valley of Arizona. Photograph by the Advance Seed Company.

lected from the susceptible WHEATLAND variety at Garden City, Kansas. Resistant strains of DWARF WHITE MILO, BEAVER, DAY, SOONER, COLBY, DARSO, and EXTRA EARLY SUMAC were selected. Resistant strains of DARSO and QUADROON were developed by hybridization. Many resistant varieties, including PLAINSMAN, CAPROCK, MIDLAND, KALO, EARLY KALO, NORGHUM, RELIANCE, and REDLAN came from hybrids involving susceptible Milos. The lines were tested on infested soil before the final choice was made.

The development of resistant varieties was so simple and effective that losses from Milo disease have been practically eliminated. A few susceptible varieties, COLBY, WHEATLAND, and BLANKENSHIP, are still grown to some extent, but largely on land that is not infested appreciably. Resistant strains of these are available where needed.

The reduction in yield from Milo disease has ranged from a trace to a total crop failure, depending upon the degree of soil infestation and to some extent on environment. Soil infestation usually builds up where susceptible varieties are grown continuously or in short rotations. On irrigated land the third successive crop after infection was first observed often has failed completely. On dry land the disease usually develops more slowly, and complete failure is less frequent. However, insidious damage, ranging from 10 to 50 per cent of the crop without the grower being aware that a disease is present, has caused the greatest total loss. Such partial damage often is mistaken for injury from drought, chinch bugs, or improper cultural methods. Average losses of about 14 bu. an acre occurred in experimental plantings on diseased areas at Chillicothe and Lubbock, Texas (Quinby and Karper, 1949). The growing of Milo would have been doomed if resistant varieties had not been developed. Other sorghum groups that are resistant could have been grown, but these were less popular than Milo. Crop rotation is ineffective for control, because the fungus remains viable in infested bare soil for at least seven years. Soil sterilization is effective but too costly.

The identification of *Periconia circinata* as the causal organism of Milo disease was not accomplished until after the disease was brought under control. Other fungi, particularly *Gibberella fuji-kuroi* and *Pythium arrhenomanes*, which cause seedling blights, were commonly isolated from plants having Milo disease, but cultures of these did not produce Milo disease symptoms. *Periconia circinata* was not considered to be a parisitic fungus until its ability to attack Milo was discovered (Leukel, 1948). Susceptible Milos are injured even by toxins that remain in soil that has been steamed to kill the fungus.

A dwarf selection from the LEOTI-ATLAS cross at Hays, Kansas, that has not been released, is highly resistant to sorghum rust caused by *Puccinia purpurea,* as well as to bacterial leaf blights. A physiological disorder, called weak-neck, results from the early drying of the peduncle followed by decay which allows the heads to break over readily. MIDLAND, which is nearly free from weak-neck, was released in Kansas in 1944 to replace susceptible varieties such as COLBY and EARLY KALO. Tests of varieties for reaction to three races of covered kernel smut (*Sphacelotheca sorghi*), two races of loose kernel smut (*S. cruenta*), and Johnson grass smut (*S. holci*) showed that SPUR FETERITA was resistant to all of the smuts. This variety was crossed with BLACKHULL KAFIR, which is susceptible to all except the Johnson grass smut. Resistant segregates of this cross were backcrossed to Kafirs and combine-type Kafirs resistant to smut were selected at Manhattan, Kansas. None of these has been released to growers.

All of the Milos and the combine types derived from Milo that were released before 1945 were susceptible to chinch bug injury. The breeding of COMBINE KAFIR 44-14 and REDLAN in Oklahoma (Davis and Sieglinger, 1952) and of COMBINE KAFIR 60 in Texas provided the first combine varieties for safe growing where chinch bugs abound. This area includes central and west central Oklahoma and the eastern thirds of Kansas and Nebraska. Thus the area in which combine grain sorghums are adapted was enlarged by some 100,000 square miles.

2. *Improvement oj Forage Sorghum*

Before 1928, all domestic sorgo varieties, except the rarely grown DENTON, had brown seeds that were bitter in taste. Livestock throughout the Great Plains ate the unpalatable seeds when fed sorghum fodder. Surplus seed left over from planting had little market value because of its low palatability. The animals were able to utilize the bitter seeds but did not appear to like them. I. N. Farr, of Stockton, Kansas, a farmer and amateur sorghum breeder, crossed SOURLESS sorgo with the palatable white-seeded BLACKHULL KAFIR. Seed from the F_1 plants was given to the Fort Hays Experiment Station at Hays, Kansas. The progenies matured too late for the dry uplands of western Kansas, and selections of the material were shifted to the state experiment station at Manhattan, Kansas, where the environment was suitable. A white-seeded, sweet-stalked selection chosen by Dr. John H. Parker was increased and released under the name ATLAS. Its seeds are very palatable to livestock and birds, and ATLAS is still a leading variety for silage and fodder in the zone from eastern Kansas and Nebraska, eastward (Fig. 2).

The full development of ATLAS is not attained under drought or short-season conditions, which require earlier and smaller varieties. A selection from a cross between ATLAS and EARLY SUMAC was released under the name NORKAN. It combines the white seed of ATLAS with the earliness of EARLY SUMAC and is adapted to the high dry sections of western Kansas. A variety intermediate between ATLAS and NORKAN was needed for north central Kansas and the uplands of eastern Nebraska. This was provided by AXTELL, a variety selected from ATLAS by a Kansas farmer but distributed by the Kansas and Nebraska Agricultural Experiment Stations.

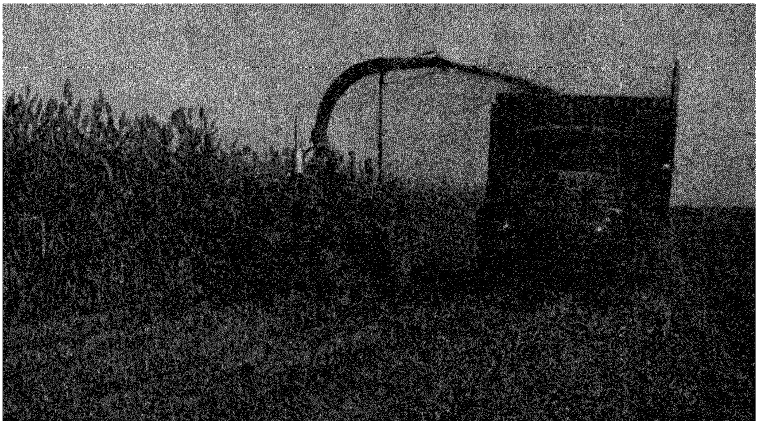

FIG. 2. A field of ATLAS being harvested for silage in Kansas with a field cutter. Photograph by Kansas Agricultural Extension Service.

ELLIS, selected from an ATLAS-LEOTI cross, provides a white-seeded variety for southwestern and central Kansas. None of these varieties is especially well adapted to Texas and Oklahoma. However, YELLOW SUMAC 108, bred at Chillicothe, Texas, has palatable yellow seed and is adapted to the panhandle sections of those states. Varieties with palatable seed are needed for several areas.

The leaves of all sorghums contain dhurrin, a cyanogenetic glucoside that may release prussic acid. Up to about 15 years ago all known varieties could produce sufficient prussic acid at times to poison ruminants that ate the green leaves. Tests of selected plants in South Dakota revealed inherent differences in prussic acid content. One low-acid strain of DAKOTA AMBER sorgo was released in South Dakota under the designation, 39-30-S. A few years later a higher yielding later variety, RANCHER, was released (Franzke, 1945). The latter variety has replaced much of the BLACK AMBER formerly grown in South Dakota and Nebraska. Other strains low in prussic acid have been developed in Nebraska. When these are released, adapted varieties will be available for most of the northern half of the United States, where sorghum poisoning usually occurs.

LEOTI sorgo has the tan plant color which is associated with resistance to three bacterial leaf blights. The ELLIS variety mentioned above, which was selected by A. F. Swanson at Hays, Kansas, inherited the tan plant color and the resistance to bacterial leaf blights. ELLIS produces a clean bright forage and palatable seed. The seed is waxy and could be used for special industrial purposes.

3. *Improvement of Sudan Grass*

LEOTI sorgo was crossed with Common Sudan grass at Chillicothe, Texas, and by G. W. Burton at Tifton, Georgia. Backcrossing of selected segregates resulted in the development of SWEET SUDAN in Texas (Karper, 1949) and of TIFT SUDAN in Georgia. Both of these varieties are resistant to bacterial leaf spots. SWEET SUDAN is resistant to Charcoal rot, and TIFT is resistant to Helminthosporium leaf blight and the gray spot disease. Common Sudan is susceptible to all of these diseases. SWEET SUDAN has sweet juicy stalks that are much more palatable than the dry nonsweet stalks of Common Sudan. Sudan grass was selected for low prussic acid content at the Wisconsin Agricultural Experiment Station. A nonpoisonous strain was crossed with TIFT SUDAN to produce the PIPER variety, which is nonpoisonous and also disease-resistant. Selection from Sweet Sudan crosses at the Kansas Agricultural Experiment Station resulted in the GREENLEAF variety, which is disease-resistant and which makes a rapid growth after the first crop is cut. These four improved varieties are largely replacing Common Sudan. They are equal or superior to Common Sudan in yield when diseases are light and greatly superior when diseases are abundant.

4. *Improvement of Broomcorn*

LEOTI sorgo was crossed with BLACK SPANISH BROOMCORN by J. H. Martin at Arlington, Virginia. Selections of this material by C. M. Woodworth at the Illinois Agricultural Experiment Station resulted in the release of OKAW and STAYGREEN BROOMCORN varieties. These varieties are resistant to bacterial leaf blights and anthracnose. Another improvement in broomcorn was the breeding of the FULLTIP (MILLER'S NO. 8) variety by J. B. Sieglinger in Oklahoma. FULLTIP produces the high quality of fiber of the SCARBOROUGH parent but with better, and therefore more economical, seed production. Also the brush is borne well out of the sheath, reducing damage from red stain when damp weather occurs shortly before harvest (Martin, 1945).

5. *Expansion of Grain Sorghum into Short-Season Environment*

For many years the safe production of grain sorghum was limited to sections having a frost-free period of 160 days or more and an average July temperature of 75° F. or higher (Martin, 1941). MANCHU and ALTAMONT KAOLIANG, selected from varieties introduced from Manchuria, were released to growers from 1910 to 1916, after it was determined that they would mature in South Dakota and northeastern Colorado. They passed out of production after brief trials, and a subsequent release in South Dakota about 1920 suffered the same fate. FETERITA, a quick-maturing type introduced from the Sudan region, was released about 1912. It was grown on a considerable acreage in Kansas, Oklahoma, Texas, and New Mexico and on a small acreage in Nebraska and Colorado. It spread to South Dakota about 1930, where it was grown in the south central part of the state. Both Kaoliang and common Feterita had certain characteristics that made them unpopular with farmers. Their stalks were dry and not desirable for fodder, and were too tall for combining. Kaoliang seed was brown and unpalatable. Feterita seeds were soft and subject to rotting in cold soil, with the result that field stands were uncertain.

SOONER, COLBY, and DAY MILOS were bred by J. B. Sieglinger at Woodward, Oklahoma, from a cross between Dwarf Yellow and Early White Milos. The latter parent was early and was grown on a small acreage in Texas but was too tall to be popular. The new varieties were shorter than either parent, COLBY and DAY usually growing to a height of only about 2 ft. SOONER was released to farmers for trial about 1931 without any fanfare, but by 1934 it was grown widely from Texas to South Dakota. It often was the only variety to mature any grain in many drought-stricken areas of the Southwest during the thirties. The distribution of SOONER in South Dakota added that state to the commercial grain sorghum region.

Much of the SOONER was replaced by COES, and more recently all grain sorghum varieties in South Dakota were displaced by the NORGHUM and RELIANCE varieties which originated in that state. These varieties are finding a place in Nebraska and Colorado and also in states to the south for late planting. Commercial grain sorghum production in northeastern Colorado was established with the release of COES, which originated at the Akron Field Station in that state. Nebraska came into the grain sorghum region with the release of EARLY KALO, which had been bred in Kansas. Later, DAY, originated at Woodward, Oklahoma, was released in Nebraska. Both EARLY KALO and DAY have since been replaced by other varieties such as MARTIN, MIDLAND, COES, NORGHUM, and RELIANCE. In northwest Kansas, corn was an important row crop before adapted quick-maturing grain sorghum varieties were available. Now, most of this acreage has been replaced by sorghum, the grain varieties being chiefly COLBY, MIDLAND, and COES. Other quick-maturing varieties released include DOUBLE DWARF WHITE SOONER, DOUBLE DWARF YELLOW SOONER, EARLY HEGARI, BONITA, COMBINE 7078, and GURNO. Together, these quick-maturing varieties have established grain sorghum over an area of some 200,000 square miles in northern latitudes or high altitudes where the frost-free period is too short for the safe growing of the later varieties formerly available.

6. Changes in Farm Practice in Sorghum Growing

Early experiments (Martin and Sieglinger, 1929) showed that thin spacing of grain sorghum was preferable under conditions of limited rainfall and that heavy-tillering varieties could be planted thinner than those that usually produced a single stalk per plant. Farm experience established thick planting for irrigated areas. Rates of 8 to 15 lb. per acre under irrigation were common as compared with 2 to 5 lb. in semiarid regions. Under irrigation the rows even of heavy-tillering varieties usually are spaced from 24 to 36 in. apart as compared with 40 to 42 in. on dry land (Fig. 3). The advent of dwarf single-stalked combine type varieties focused attention upon the need for information on proper spacing. Experiments were started to test the requirements for such new varieties about 25 years ago. It soon became evident that closer row spacing or thicker planting was possible for the smaller plants but that yields were not increased under semiarid conditions by planting more than about 5 lb. per acre. Sharp responses to thick planting were obtained under irrigation. Experiments on irrigated land at Garden City, Kansas, showed that WESTLAND, a single-stalked combine type, yielded about 30% less than FINNEY. In a subhumid area at Manhattan, the yields of MIDLAND have been increased about 25 per cent, as a 10-year average, by spacing the rows 20 in. apart as compared with 40 in. spacing.

The drilling of sorghum in close rows has not been recommended by research agencies despite fair success with that method in experiments. Close drilling courts crop failure under drought conditions, and the lack of intertillage permits weed competition on foul land. The use of chemical herbicides has eliminated some of the weed hazard, and early harrowing also helps to control weeds in drilled sorghum. Despite the above risks, the growing of combine grain sorghums in drilled rows about 10 to 18 in. apart is becoming very popular, especially in Kansas and New Mexico. This practice permits the growing and harvesting of the crop entirely with the machines used in wheat production, and the time-consuming intertillage is omitted. Wheat growers thus can shift to grain sorghum without additional expense, and this practice has favored a large sorghum acreage in years when wheat prospects are unfavorable.

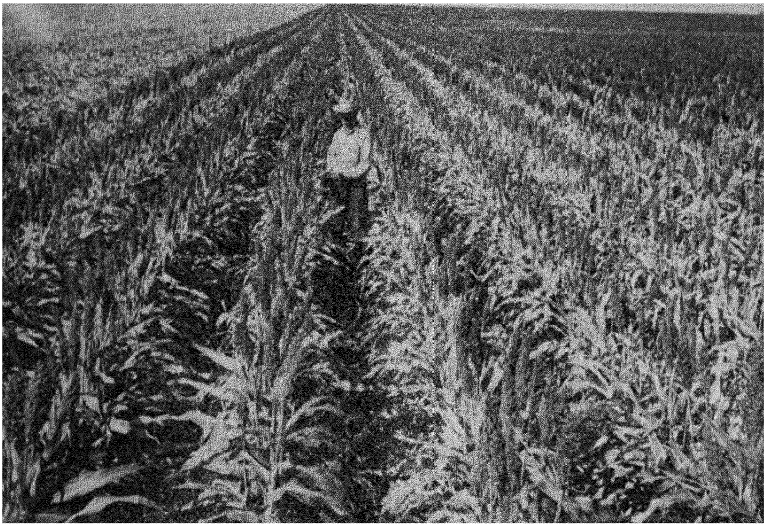

FIG. 3. A field of REDBINE 60 growing under irrigation on the South Plains of Texas.

Much of the sorghum ripens in the fall when cool weather retards the ripening of the grain. North of Oklahoma the crop usually is combined after freezes have killed the plants, which stops water intake and allows the grain to dry to some extent. Despite this, much of the combined grain is too high in moisture content for safe storage. Most of the crop matures too early to permit the postponing of harvest until after the first frost. The usual delay of from three to six weeks between ripening and frost would cause losses from lodging of the stalks, weathering of the grain, and bird depredations. The better drying weather at maturity in the South does not compensate for the continued water uptake by the live plants. Thus high-moisture grain sorghum is a source of difficulty wherever the crop is grown. Some damp grain sorghum can be preserved in outdoor bins during the cold weather that follows late harvest if it is fed or otherwise disposed of before warm weather arrives. Sometimes the threshed grain is dumped on the ground in narrow ricks to permit natural drying. Drying in ventilated bins often is effective in the drier sections for grain that contains no more than 15 to 16 per cent moisture. Wind-pressure cowl ventilators on the top of ventilated bins give the most effective drying of any system of bin drying that does not employ artificial air circulation. Farm bin-grain drying with forced air draft, with or without supplemental heat, is coming into practice. Central grain dryers for drying grain sorghum on a custom basis at marketing points or in producing areas are becoming more numerous, especially in southern Texas. Thus the development of drying facilities following co-operative research has solved much of the difficulty that formerly retarded the production of grain sorghum for the market in many sections (Shedd and Walkden, 1947; Sorenson *et al.*, 1949).

7. *Sorghum in Industry*

Until 1943 grain sorghum was primarily a crop for local feeding, and the portion that was shipped to terminal markets was used in poultry feeds and mixed livestock feeds (Martin and McMasters, 1951). Two waxy (glutinous) varieties, WAXY KAFIR and CODY, bred respectively by R. E. Karper in Texas and by A. F. Swanson in Kansas, were released for production about 1943. The grain was dry milled, followed by starch extraction to produce a substitute for minute tapioca until cassava starch again became available after the war (Martin and Jenkins, 1951). A waxy variety called MILOCA, bred by R. E. Karper in Texas, was released about three years ago. The research and development needed before starch manufacture from sorghum grain was feasible was conducted largely by the General Foods Corporation and the Nebraska and Kansas Agricultural Experiment Stations. Further research by the Corn Products Refining Company at Argo, Illinois, assisted by the Midwest Research Institute at Kansas City, Missouri, perfected processes for wet milling. This was followed by the building at Corpus Christi, Texas, of a sorghum-starch mill with a capacity of 6 million bu. of grain annually, which began operating in 1948. Further research at the Kansas Agricultural Experiment Station culminated in the establishment of a sorghum flour mill at Dodge City, Kansas. The flour is used as an adhesive for the manufacture of gypsum board.

An additional recent sorghum industry is the dehydration of whole sorgo plants to produce a meal, high in sugar content, as an ingredient in mixed feeds. Several mills in Kansas and Texas are producing the dehydrated meal. The research involved in developing this product was conducted by the Western Star Milling Company of Salina, Kansas, with assistance from the Kansas State Board of Agriculture and the Fort Hays (Kansas) Experiment Station (Swanson, 1951).

III. LIMITATIONS OF SORGHUM VARIETY YIELD TRIALS

A quarter-century ago it became evident that relative varietal yields depended upon obvious attributes such as plant size, head size, growing period, tillering capacity, and resistance to insects and diseases. Actual yield, naturally, is modified by differences in soil moisture supply, length of growing season, temperature, day length, and soil fertility, and by cultural practices, such as planting date and plant spacing. Varietal yield rank in a given test likewise varies with the above conditions. Such responses were evident in numerous varietal tests conducted under different conditions at the same station and in different seasons. The testing of varieties under different conditions at the same station aided in the adoption of (1) such practices as late planting for quick-maturing varieties, (2) thicker planting for nontillering varieties, (3) quick-maturing varieties and thin planting for droughty conditions, and (4) close spacing or the use of heavy-tillering later varieties for irrigated fields and well-watered bottom lands.

Sorghum varieties are so strikingly sensitive to environment that their computed average yields on a regional basis are likely to be merely compilations of nonhomogeneous data. Under a climate as variable as the Great Plains, the results of varietal tests reflect average or "normal" expectations in not more than one-half of the years. In the remainder, the best varieties are those suited to drier or wetter, or longer or shorter, than normal seasons, or to the presence or absence of certain insect pests.

Sorghum can be grown with some degree of success anywhere in the world where the summer temperature averages 65° F. or higher, with a frost-free period of 120 days or more and with an arable soil supplied with sufficient moisture to grow any field crop. Sorghum thrives on soils ranging in texture from light sands to heavy clays and in reaction from pH 4.5 to 8.5.

BLACK AMBER sorgo has been grown in every state in the U. S. Other varieties outyield it wherever a longer growing season, more abundant moisture, or shorter photoperiod permit later and larger varieties to thrive. The approximate yield, rank and the probable area of adaptation of a variety can be predicted with fair success by observing its characteristics when grown in comparison with varieties of known performance.

Yield tests are necessary to assure that a new variety will perform satisfactorily. Such tests in different seasons or under different conditions also reveal the disease, insect, and environmental reactions of a variety. A few varieties such as RED KAFIR, CLUB KAFIR, and AJAX were released wholly because of their high yields in experimental plot tests. They were soon dropped by growers because of certain defects of the varieties that were more critical on farms than in experimental plots. Slightly lower yielding varieties, lacking serious practical defects, maintained their popularity on farms for many years.

When sorghum is grown for fodder or silage in intertilled rows by usual methods, such varietal qualities as suitable maturity, juiciness, sweetness, and palatability are important. These desired characteristics, together with uniform growth, can be assured by the proper choice of pure seed of recommended varieties. Forage varieties grown in cultivated rows with the plants spaced at a customary distance of 2 to 6 in. apart in the row give yields directly proportional to their plant size. Varieties with the same maturity factors and tillering capacity give yields proportional to the plant height. The yields of varieties with the same genetic factors for internode length are proportional to the relative length of their growing periods. These relationships are evident in most seasonal varietal tests in which all varieties have the opportunity to reach full development, and almost invariably so when the yields for several years are compiled. Such tests also have shown that forage sorghums of similar plant size and maturity yield approximately the same as would be expected. The actual plant size of a given variety may be increased by longer days (actually shorter nights), ample soil moisture and soil fertility, and optimum growing temperatures.

A variety moved southward into zones where the nights are longer but with other growing conditions equally favorable produces smaller plants because the vegetative period is shorter. WACONIA AMBER sorgo averaged 14 tons green weight per acre in one year in southern Minnesota. It has never attained such yields under the more favorable temperature conditions in Texas, where the nights are too long for such an early variety.

The relation of growing period to forage yield is shown in Table II (Swanson and Laude, 1942; Quinby *et al.* 1934). It should be noted that the growing period of ATLAS averaged 10 days less at Chillicothe, Texas, than at Hays, Kansas, where summer nights are shorter.

The best yielding varieties for a given environment are those with the longest growing period that still permits the plants to attain the desired stage of maturity. The grower, however, considers many plant characteristics other than yield such as ease of handling, palatability, stalk stiffness, resistance to disease, and desired time of harvest. Only

TABLE II

Relation of Growing Period to Sorghum Yield

Variety	Cured forage yield, tons/acre	Days to mature
Hays, Kansas (18-year average, 1924-41)		
ATLAS	3.21	123
LEOTI	2.86	110
EARLY SUMAC	2.65	107
Chillicothe, Texas (6-year average)		
HONEY	5.12	132
ATLAS	3 87	110
SUMAC	3.73	107
EARLY SUMAC	3.18	97

quick-maturing varieties reach the desired stage of development in sections with a short growing season, low summer temperatures, or limited soil moisture. Since drought prolongs the vegetative period of sorghum, later varieties are needed for irrigated or stream bottom lands than for dry upland fields, even on the same farm. In much of the sorghum-growing area, farmers often favor varieties that yield somewhat less than the most productive one because they are easier to handle. Thus SUMAC sorgo is preferred to the taller more productive HONEY variety in Texas; ATLAS replaced the more productive KANSAS ORANGE variety in eastern Kansas; and ELLIS replaced the more productive LEOTI variety in western Kansas. In each case the favored variety was less subject to lodging. Likewise many growers in Arizona, New Mexico, and western Texas prefer the less productive HEGARI for forage to the taller, higher yielding recommended sorgo varieties. Many farmers in western Kansas grow Kafirs or TRICKER SORGO in preference to more productive sorgos. The taller, higher yielding varieties are more likely to lodge and are more difficult to harvest with a corn binder. Shocking, hauling, stacking, and feeding require from six to eight hand operations, all of which are easier with short-stalked but low-yielding varieties. Consequently, where hand labor must be hired, it may be more economical to grow more acres of a low-yielding variety, because all field operations up to harvest may be done with a tractor. Furthermore, sorghums that do not exceed 6 ft. in height can be harvested three rows at a time with a grain binder, whereas taller varieties must be cut with a one-row corn binder.

Varieties that lodge are regularly discarded in favor of stiffer stalked varieties that yield no more or even considerably less. FREMONT has replaced much of the BLACK AMBER formerly grown in northeastern

Colorado and western Nebraska, largely because of its stronger stalks.

When sorghum is grown for silage, the highest yielding variety may not be preferred, even when it is to be cut with a field silage cutter. Field silage cutters designed for a 15-ton yield of corn silage have been subject to frequent breakdowns when cutting sorgo yielding from 20 to 30 tons an acre. Such yields are readily obtained on rich irrigated lands of the Southwest. A sorghum with a high yield record at Chillicothe, Texas, where it originated, was not released there because no farmer could be found who wanted to grow such a large variety. Recently the variety was reselected at Meridian, Mississippi, and released in that state for sirup production under the name TRACY. Since sorghum for sirup usually is cut, stripped, and topped by hand, large-stalked varieties are even advantageous. Furthermore, TRACY is being recommended for silage in Mississippi, because recent field silage cutters have been strengthened so that they can handle a heavy crop.

When sorghum is drilled thickly for hay production at rates of from 15 to 75 lb. per acre in the Great Plains, any variety exhausts the available soil moisture except in wet years. The yield of dry matter then is limited by the moisture supply, and small or large varieties yield nearly the same (Vinall *et al.*, 1924). Farmers in the central Great Plains, Kansas, have recognized this situation for nearly a half-century. For the production of drilled sorghum hay or "sowed feed" they often purchase nondescript so-called "mixed fodder cane" for seed, knowing that it will yield approximately the same amount and quality of hay as does the best certified variety.

Drilled sorghum also is so thick that the plants develop very few seeds, and even the sweetest varieties have little opportunity to store sugar in the stalks. Any sugar in the stalks is lost during the several weeks required to cure a thick-stemmed grass like sorghum. Since the hay loses its sugar and juice during curing, there also is no advantage in growing a sweet, juicy variety.

The yields of single-stalked grain sorghum varieties are directly proportional to head size when the plant distribution is the same. The relative head size of single-stalked varieties is proportional to the length of the growing period for the variety, with occasional exceptions. The head size is affected by environment, which may favor either an early or late variety, depending upon the plant stage at which critical conditions occur in a particular season. Earlier and smaller varieties usually make the best grain yields in dry years.

STANDARD BLACKHULL KAFIR with its larger heads and longer growing period (131 days) averaged 4 4 bu. per acre more than TEXAS BLACKHULL (111-day maturity) in two years of good rainfall, whereas the latter yielded 9.7 bu. more in four subsequent drier years at Lubbock. Texas (Karper *et al.*, 1932).

Varieties that tiller freely normally have smaller heads than do single-stalked varieties of the same maturity, but the additional heads compensate for the smaller size. Tillering is advantageous when the plant stand or row spacing is inadequate to provide sufficient heads of a single-stalked variety for maximum yields. Tillering also may increase yields when adverse conditions affect the main stalks, leaving late tillers to provide most of the crop. Good first-generation hybrids bear much larger heads than do nonhybrid varieties of the same maturity. An occasional variety, such as KALO, also may produce larger heads and consequent larger grain yields than other varieties of the same maturity, as shown by yields of KALO and TEXAS BLACKHULL KAFIR in Table VI. However, such heads usually are too heavy for the stalk on which they are borne, and lodging losses offset the gain in yield. Suitable hybrids produce a stalk that is sturdy enough to support a relatively large head.

IV. SORGHUM INTRODUCTION

Africa is believed to be the native home of sorghum, but the crop has been cultivated since ancient times in the Near and Middle East, in India, China, and Manchuria. The species is a modern immigrant to the Americas and Australia. Accounts of the early introductions and work with sorghum have been presented by Vinall *et al.* (1936) and Martin (1936).

Introduction of sorghum varieties into the Americas began with the slave trade, when grain was brought along as food. The progenitor of the Milo varieties probably reached South America in such a manner and was subsequently introduced into South Carolina. Other varieties brought in with slaves failed to survive as cultivated varieties, but "chicken corn" was growing as a weed in corn fields along the Ohio river as late as 1935.

There were several introductions of varieties that influenced the present status of varieties in the United States. The first sweet sorghum or sorgo that reached the United States came from China by way of France in 1851 and was distributed as CHINESE AMBER by the United States Department of Agriculture in 1857. The present day varieties of ORANGE, SOURLESS, GOOSENECK, WHITE AFRICAN, SUMAC, STRAIGHTNECK, and HONEY are the varieties that survived from an introduction of 15 varieties that were first grown under their Zulu names after being brought into the United States by Mr. Leonard Wray, an English sugar planter from Natal, South Africa. The United States Department of Agriculture introduced the COLLIER variety from Natal, South Africa, by way of England in 1881, the PLANTER variety from Africa by way of India and Australia in 1888, and MCLEAN sorgo from Australia in 1891. The present American sorgo varieties originated from CHINESE AMBER, the 15 varieties introduced by Leonard Wray, or COLLIER, PLANTER, or MCLEAN. A recent introduction from the Sudan region by the United States Department of Agriculture was released in 1951 in co-operation with the Mississippi Agricultural Experiment Station from Meridian, Mississippi. The variety has been named SART and is recommended for commercial syrup production in Alabama, Georgia, Tennessee, and Mississippi.

WHITE and BROWN DURRAS, called Egyptian corn or "Gyp" corn, were introduced into California from Egypt in 1874. The successful culture of these varieties established grain sorghum as a crop in the United States. WHITE KAFIR, and apparently RED KAFIR, from Natal, South Africa, were shown at the Centennial Exposition at Philadelphia in 1876, and seed from the exhibit was later distributed in this country. It is not known how BLACKHULL KAFIR reached the United States, but it undoubtedly came from South Africa and was growing on farms in Kansas about 1890. The Milo introduced into South Carolina in 1879 (Karper and Quinby, 1946, 1947b) was tall and late in maturity. Early-maturing and dwarf strains were selected by farmers, and for about 30 years prior to 1940, DWARF YELLOW MILO was the predominant grain sorghum in the Southern Great Plains. The advent of grain sorghum coincided with the building of the railroads and contributed to the settlement of the Great Plains, where corn was not well adapted.

SHALLU, a variety that is sometimes called Egyptian wheat, was introduced from India in 1890. Shortly after the turn of the century, work with grain sorghum was expanded. Large numbers of sorghum varieties were introduced by the United States Department of Agriculture. PINK KAFIR was introduced about 1904 and a few years later was widely distributed from the Ft. Hays Branch Experiment Station in Kansas. FETERITA was introduced in 1906 and HEGARI in 1908. These two varieties were distributed from the Texas Agricultural Experiment Substation at Chillicothe.

Sudan grass was introduced in 1909 by the United States Department of Agriculture and distributed in co-operation with the Texas Agricultural Experiment Station from Chillicothe. Johnson grass—the perennial relative of annual Sudan grass—was introduced by Governor Means of South Carolina in 1830. It was popularized by William Johnson of Alabama and is a pernicious weed in areas where its underground rootstocks will survive the winter. Johnson grass is a curse to thousands of farmers throughout the South but is considered to be a valuable forage plant by many others.

Benjamin Franklin is credited with the introduction of Broomcorn, as he was supposed to have grown plants from seed plucked from a broom imported from Europe. An interesting account of this crop and the manufacture of brooms has been written by Martin (1953).

Sorghum varieties continue to be introduced by the United States Department of Agriculture. Most of the varieties prove to be unadapted, and many will not produce seed, apparently because of unsatisfied temperature or length-of-day requirements. Varieties of sorghum are numerous and differ greatly in adaptation. In some tropical and subtropical climates there are two distinct growing seasons for sorghum that correspond roughly to the summer and winter growing seasons of temperate zones. The varieties that grow in one season will grow in the other but growth is modified. Many of the hundreds of introduced varieties that were found to be of no great value will mature seed, but the characteristics that made them valuable in their native habitat are of little worth under the conditions where they were tested. There is an area in the Egyptian Sudan where sorghum varieties are grown that must mature early enough to be harvested before the season of overflow. These varieties are not valuable in the present sorghum-producing area of the United States, as their durations of growth are not sufficiently long to allow adequate production. There are varieties in Nigeria that are late in maturity to allow the time of grain production to follow the rainy season. Those varieties are too late in maturity to be grown successfully in the Great Plains of the United States, because they usually exhaust the supply of soil moisture before the period of grain production. One variety, SHALLU, is grown in the area adjacent to the Gulf of Mexico from spring planting, whereas in India it is grown from fall planting. Along the Gulf coast where the variety is grown, temperatures are relatively low but still high enough to allow growth of sorghum during the early spring season when the period of daylight is close to 12 hours. There are sorghum varieties adapted to so many climatic conditions that, within the temperature range of the species, there are sorghum varieties that fit into many diverse ecological niches.

V. Plant Breeding Methods

1. Hybridization and Selection

The early activities of individuals and public agencies with sorghum were confined largely to the introduction of new varieties from abroad, to selection within existing strains, and to efforts to preserve the identity of the varieties already in existence. Numerous strains originated in the hands of farmers or on agricultural experiment stations, and several were given wide distribution by railway companies. Finally the possibilities inherent in hybridization and selection were recognized, and a new era of sorghum improvement began.

As early as 1916, H. Willets Smith, a farmer at Garden City, Kansas, had uniform strains that had been selected from a chance hybrid between Kafir and Milo. H. N. Vinall and A. B. Cron of the United States Department of Agriculture began to hybridize sorghums in 1914 and, in 1923, CHILTEX and PREMO, two selections from a Feterita × Kafir cross that resulted from this work, were distributed by the United States Department of Agriculture in co-operation with the Texas Agricultural Experiment Station. CHILTEX and PREMO were the first sorghum varieties that resulted from artificial hybridization to be released to farmers.

A method of progeny row selection was described by Vinall and Cron (1921), and it is this method that has been used in large part to produce the numerous varieties that have been distributed during the past 30 years.

2. *Technique of Selfing and Crossing*

a. Self-Pollination. Sorghum is naturally self-pollinated, but cross-fertilization occurs in varying amounts depending upon the velocity of the wind, the size of the insect population, and other factors. Cross-pollination in common sorghum has been reported to be a few per cent by Karper and Conner (1919) and as high as 70 per cent in Sudan grass by Garber and Atwood (1945). Self-pollination of sorghum is sometimes necessary and is easily accomplished by placing a paper bag over the head before blooming begins and leaving the bag in place until after the completion of blooming. The bag is usually fastened about the peduncle with metal staples but can be fastened with a paper clip or tied with a string.

If it is necessary to assure complete self-pollination or, in the case of partially male-sterile heads, to be sure that no foreign pollen falls on the head, it is necessary to leave bags on sorghum heads until maturity. In such a case, the larvae of the insect *Heliothis armigera* (Hibner), the corn-ear worm, becomes a problem. This worm, when protected from predators, as reported by Quinby and Gaines (1942), will frequently eat a large part of the grain on bagged heads of sorghum. Dahms *et al.* (1951) devised a method of controlling corn-ear worms in bagged heads of sorghum by treating the bags with the commercial insecticide, aldrin. Two or three milliliters of a 5 per cent emulsion of this insecticide poured or painted on the inside of the bag will wet a strip from top to bottom and kill any larvae that hatch under the bag or enter it later. The treated bags also protect the heads from the sorghum webworm, *Celama sorghiella* (Riley), and most aphids. The bags that have been treated with aldrin may be stored for several weeks or even months without loss of insecticidal properties. The bags used may be of any size large enough to inclose the heads. The bags need to be made of heavy Kraft paper glued with a waterproof adhesive; otherwise the bags will develop holes during rain storms.

b. Hand Emasculation and Pollination. Vinall (1926) described a process of hand emasculation and pollination of sorghum, and similar methods are in use at present. By this method, all but a few spikelets, including the pedicelled spikelets if they contain anthers, are removed from the head with dissecting scissors just prior to blooming. The anthers are then removed from the spikelets by using tweezers, a needle, a pencil point, or some other instrument. The emasculated spikelets are then protected by a small bag and pollinated at the time of blooming, which is usually on the first, second, or third morning following emasculation. A large percentage of the emasculated florets will produce seed if viable pollen is placed on the exposed stigmas. During the hot summer months, sorghum blooms during the night or early morning hours (Stephens and Quinby, 1934). However, Artschwager and McGuire (1949) have found that sorghum pollen does not germinate until daybreak. Usually enough scattered spikelets open after the time of maximum blooming to provide ample viable pollen for crossing purposes until late in the forenoon. Sorghum pollen does not remain viable for more than a few hours, and no practical method of preserving sorghum pollen has been devised. In the field. pollen is difficult to collect on windy mornings, especially from loose-panicle types, as there is enough agitation of the anthers under those conditions to cause them to be devoid of pollen soon after dehiscence. Pollen sufficient for pollinating a few spikelets can easily be collected in a petri dish and transferred to the stigmas by rubbing the coated petri dish against the stigmas. Contamination can be prevented between one pollination and the next by dipping the hands and the utensils in water.

Large amounts of pollen are needed to pollinate male-sterile heads or heads emasculated with hot water. In such a case, pollen is usually collected in a paper bag that has been placed over a head that is blooming. When the head is shaken, pollen collects in the bag. The bag is then placed over the receptive head and shaken vigorously. This method works well in many cases, but, in others, the pollen will rupture on coming in contact with other pollen grains and the entire pollen mass will become gummy. When this occurs, the only feasible way to transfer pollen is to remove the pollen-bearing head from its stalk and agitate it vigorously over the emasculated or male-sterile head.

c. Hot Water Emasculation. A method of emasculation of sorghum heads using hot water has been reported by Stephens and Quinby (1933), and this method has been adapted by others for use on several other species including rice, millet, and several range grasses. The method is useful when relatively large amounts of crossed seed are needed. The possibility of emasculation by this process exists because the pollen-producing parts are slightly more sensitive to heat than the female parts of a flower. This difference in sorghum appears to be one degree Centigrade or less. Water at 48° C. poured around a sorghum head and left for 10 minutes will destroy the viability of pollen. Water temperature is likely to be as low as 42° or 44° C. at the end of the 10-minute period. The floral parts of some varieties are slightly more sensitive to heat than others, and Milo may have to be emasculated at 47° or 47.5° C., whereas the female parts of Kafir will withstand 48° C. (Fig. 4).

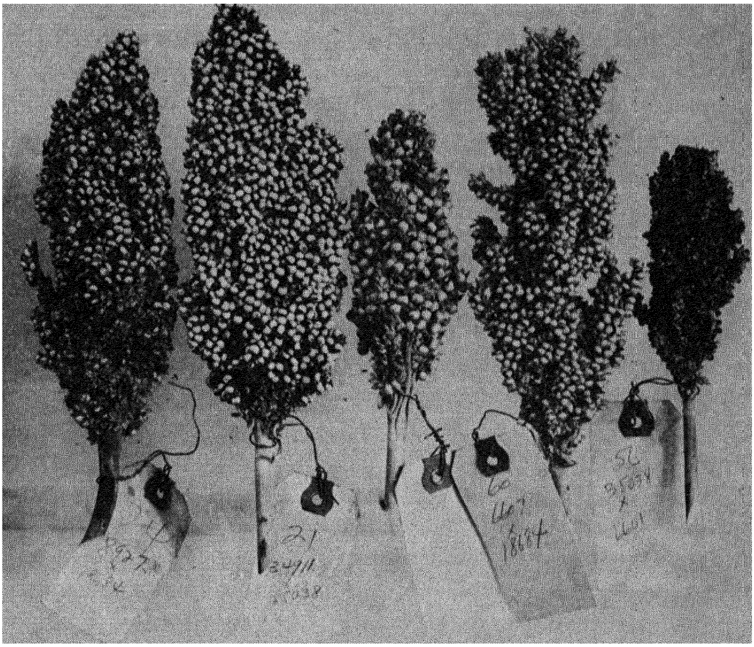

FIG. 4. Sorghum heads that were emasculated with hot water and pollinated with foreign pollen. The head on the left was emasculated with water at 47.5° C. The other four heads were emasculated at 48° C.

The hot water method of emasculation of sorghum is relatively simple but requires a supply of warm water in the field or greenhouse and success in keeping the water from leaking from the container that surrounds the sorghum head. The equipment consists of a metal container of about 1-gal. capacity to hold the water, with the base inclosed in a rubber tube and with legs to provide support. The container is placed over the sorghum head and the rubber tube fastened about the peduncle and leaf sheath of the plant. It is usually necessary to put some soil into the container to seal the openings in the tube. The head is immersed in the hot water at the proper temperature and at the end of 10 minutes the water is removed from around the head. The head is then bagged to prevent undesired pollination. Blooming is usually delayed one day by this treatment. It is advisable to use heads that are ready to bloom, but emasculation is effective several days before blooming and as soon as the head emerges from the boot. Sorghum stigmas are receptive for several days, as shown by Stephens and Quinby (1934), and one pollination will frequently result in adequate sets of seed. However, the stigmas of some varieties of sorghum are short and do not remain exposed when the glumes close at the end of blooming. On this account, it is usually advisable to pollinate each morning after blooming of the emasculated head begins, until anthesis is completed at the end of four or five days.

3. Colchicine-Induced Variants

There are many instances of polyploidy in plants resulting from treatment with colchicine, but Franzke and Ross (1952) have reported obtaining true breeding strains of sorghum unlike the parental stock in a number of characteristics by treatment of seedlings with colchicine. They do not know with certainty what processes are involved, but they have assumed that there must have been point mutation followed by somatic reduction of the chromosome number and subsequent restoration of the diploid number. They have assumed further that such a cell must take over the growing point and form homozygous tissue of a different genotype than the original embryo. Somatic chromosome reduction has been reported in *Allium cepa* by Huskins (1948).

If it is confirmed that there is somatic reduction of chromosome number and subsequent restoration of the diploid number following colchicine treatment of seedlings, such a treatment might become a helpful tool to a plant breeder even without the occurrence of point mutations. If this sequence of events does happen, it should be possible to treat F_1 seedlings and have some F_2 plants that would not segregate in later generations.

VI. CYTOLOGY AND GENETICS

1. *Botanical Classification and Cytology*

Botanists, plant breeders, and geneticists have had diverse opinions about the botanical classification of the numerous cultivated forms of sorghum, *Sorghum vulgare* Pers., including the grass sorghums. The genetic evidence at the present time, in the opinion of the authors, indicates that all of the cultivated sorghums and the grass sorghums with the somatic chromosome number of 20, comprise one extensive species. Vinall *et al.* (1936) classified the numerous American varieties of common sorghum as being of one species. Because of the diversity within the genera, Snowden (1936) thought that, as a matter of convenience, the genera should be divided into species that would correspond roughly to the groups that were recognized by agriculturists. Snowden's classification is not perfect in this respect, since such diverse agronomic varieties as HEGARI, BLACKHULL KAFIR, and ORANGE sorgo are included within the species *S. caffrorum*, and Broomcorn and several sorgos within *S. dochna*. After examining the 3000 forms in the world collection of sorghum at Kew Gardens, Snowden classified the genera into 6 subseries and 31 species. Laubscher (1945) was not willing to classify all the cultivated sorghums into one species, because he thought that he recognized different modifier complexes, but he was not willing to admit the justification for a division into 31 species. His work led him to bebelive that there is genetic support for a division of the cultivated sorghums into "races." It is presumed that "races" would consist of such groups as the Kafirs of South Africa, the Feteritas of the Egyptian Sudan, the Durras of the Near and Middle East, the Shallus of India, the Kaoliangs of China, Manchuria, and Japan, the Broomcorns and many others in tropical Africa and in India. Strains from these groups of varieties have been crossed and segregating populations studied in the United States. Such quantitative characters as height and even duration of growth in many instances are relatively simple in inheritance. These "races" exist but apparently not because of different modifying complexes.

Alleles for sweet and juicy stems and two alleles for glume color were easily transferred from LEOTI sorghum to Sudan grass by Quinby, Karper, and Stephens, and an improved variety was distributed under the name of SWEET SUDAN grass by the Texas Agricultural Experiment Station and the United States Department of Agriculture as reported by Karper (1949). R. E. Karper has numerous selections among his breeding strains at Lubbock, Texas, in which there is a mixture of characteristics from sorghum and Tunis grass, sorghum and Sudan grass, and sorghum, Sudan, and Johnson grass. There is evidence in this material of the homology of chromosomes in sorghum, Sudan grass, and Tunis grass. Johnson grass, with a somatic number of chromosomes twice as great as the others, evidently has chromosomes or parts of chromosomes that are homologous with those of common sorghum and Sudan and Tunis grasses.

Cytotaxonomic studies have led Garber (1950) to divide the genera *Sorghum* into six subgenera of which Eu-sorghum is one. Eu-sorghum consists, in this classification, of *Sorghum vulgare,* the common sorghums and the grass sorghums, Sudan, Tunis, and Tabucki among others; and *Sorghum halapense,* which is Johnson grass. Duara and Stebbins (1952) and Hadley (1953) have concluded that Johnson grass is a segmental allopolyploid which arose from a cross between two species closely related cytologically.

The genetic and cytological evidence seems to indicate that the cultivated varieties of sorghum and the grass sorghums with the somatic chromosome number of 20, constitute one large and varied species. If this is so, it should be possible to transfer desirable characters almost at will among the numerous sorghum and grass sorghum varieties.

The genetics work with sorghum is not as extensive as that with several other species, but what there is of it suggests that relatively few alleles control some of the vital growth processes that differentiate varieties.

2. *Inheritance in Sorghum*

Information on the genetics of sorghum has been accumulating since 1916, when Graham (1916) reported on seed color inheritance. Most of the work has been done in India and in the United States of America since 1920. Since most Indian varieties will not mature consistently in this country, it is difficult to make good use of some of the information that has come out of India. The literature concerning some characters is confused, and at present there is not enough information in existence to bring order out of chaos. Martin (1936) summarized the genetics literature of sorghum prior to 1935. The following review of sorghum genetics literature does not include many of the characters included in the summary by Martin, but does make an attempt to interpret the information that is available on characters that affect production, adaptation, or economic value.

A knowledge of the anatomy and morphology of sorghum is an aid to understanding some of the genetics of sorghum. Work in this field has been reported by Artschwager (1948) and Artschwager and McGuire (1949), and the pertinent literature is cited by them.

a. Seed Color. The genetics of seed color in sorghum has received attention from a number of workers. The colors, which are of some economic importance, are varied and occur in different layers of the caryopsis. The contrasting colors such as white, yellow, red, and brown occur as a result of the color content of the epicarp, the thickness of the mesocarp, the presence or absence of a brown testa, and the dominant or recessive condition of a gene designated as *S*, that controls presence or absence of brown pigment in the epicarp when a brown testa is present. The genetics of some of the colors is not understood, and it is not yet time to make an effort to reconcile conflicting statements in the literature.

(1) Epicarp colors. There are reports of six genes, exclusive of the *S* gene, that cause color in the epicarp. The first two were reported by Graham (1916) in India. These two genes influence the color of the plant sap, and the colors show in the dead leaf tissue and the anthers as well as in the mature grain. In live leaf tissue or immature grain the colors are masked by chlorophyll. Graham accounted for the ratios of red, yellow, and white he obtained in segregating populations by assuming two genes, *R* for red and *Y* for yellow, both of which must be present for the development of red seed color. The genotypes of the three colors would be *RRYY*, red; *rrYY*, yellow; and *RRyy* and *rryy*, white. In this scheme, it is the heterozygous condition of *Y* rather than *R* that gives simple segregations for red and white seed. Dihybrid segregations give ratios of 9 red, 3 yellow, and 4 white.

Ayyangar *et al.* (1933b) suggested a different set of symbols and, in addition, reported a third gene that was called *I*. This gene in the dominant condition intensifies color and differentiates between red and pink when both *R* and *Y* are present in the dominant condition. Using Graham's designations for *R* and *Y*, Red Kafir is *RYI* and has dark red colored seeds, and the Yellow Milos are *RYi* and are genetically pink but have been called yellow in the United States. True yellow that is *rrYY* is not represented by a commercial variety in the United States.

In addition to the *I* factor, Ayyangar *et al.* (1934b) also reported two genes that in the dominant condition cause a brown tinge in the pericarp. These genes might well be designated as BW_1 and BW_2. These brown washes are common in Indian varieties but are not encountered in the varieties of African origin grown in the United States. Ayyangar and Nambiar (1938) also reported an intensification of color independent of the three major factors, and this gene was assigned the designation of *M*.

It is not known in the United States at present how some pericarp colors are inherited. It is not known if the pink pericarp color of the

Pink Kafirs can be explained as some combination of the dominant or recessive genes *R*, *Y*, and *I*. Also some colors come out of crosses between WHITE MILO, BONAR DURRA, and DURRA PI 54484 that do not fit into the *R*, *Y*, and *I* scheme. It is possible that the factor *M* of Ayyangar and Nambiar (1938) may play a part.

(*2*) *Brown testa color.* A thick layer of brown cells immediately outside the aleurone has been called subcoat or undercoat and is the inner integument or testa. Sieglinger (1924) first reported on the inheritance of this seed layer, and Stephens (1946) and Laubscher (1945) have reported that two genes control the presence or absence of the testa and both must be present in the dominant condition if the layer develops. Now that two genes are known to control presence or absence of the testa, it is logical to follow the suggestion of Stephens (1946) and call the two factor pairs B_1b_1 and B_2b_2.

Ayyangar and Krishnaswami (1941) have reported that the testa is present in some sorghum varieties without containing brown pigment. Apparently the absence of brown pigment occurs in cases in which the testa was not completely absorbed. If the testa is ever present and fully developed and is still void of brown pigment, there would apparently be a gene, and not one of the *B* genes, that would control presence or absence of color. In such a case the B genes would control the presence or absence of a testa and not the presence or absence of the brown pigment in the testa. It is obvious, however, that the testa when present is usually brown.

(*3*) *The S gene.* When the brown testa is present, the epicarp of varieties or hybrids is brown if a gene *S* is present in the dominant condition. Vinall and Cron (1921), Sieglinger (1924), and Swanson (1928) have described the action of this gene differently. Ayyangar and Krishnaswami (1941) examined the seeds of 48 varieties and found in most cases that seeds with a brown testa and a brown epicarp had brown color in the mesocarp. However, strains AS5195 and AS3356 that had brown in both the testa and epicarp had no color in the mesocarp. On that account, it would be unwise to assume that the dominant *S* gene allows the brown pigment that originates in the testa to spread to the outer layers, as, in such a case, it would be difficult to explain the occurrence of a mesocarp without brown pigment when the layers on each side are pigmented. It seems only safe to assume that dominant *S* in the presence of dominant B_1 and B_2 allows brown to be present in the epicarp. Recessive *s* prevents the presence of brown in the epicarp in the presence of dominant B_1 and B_2.

(*4*) *Pearly and chalky grains.* Ayyangar *et al.* (1933c) reported on the inheritance of pearly and chalky grains in sorghum and assigned the symbols *Zz* to the factor pair. In their populations, the dominant condition of the *Z* gene produced a thin mesocarp, and the seeds had a pearly appearance. The recessive condition, *z*, produced a well-developed mesocarp, and the seeds were chalky white in color. Swanson (1928) assumed that the factor pair *Ss* controlled the thickness of the mesocarp, and Sieglinger (1924) reported that the recessive condition of *s* produced pearly grains. It appears that the gene *S* controls only the presence of the brown pigment in the epicarp and that the *Z* gene of Ayyangar *et al.* (1933c) controls the thickness of the mesocarp.

(5) *Seed colors that are caused by mechanical injury or weathering.* Swanson (1928) and Ayyangar and Krishnaswami (1941) have reported that spots on some white seeds are caused by underlying fragments of the testa. This sort of spotting occurs in case a plant that is recessive for either b_1 or b_2 has a fragment of the testa that persists to maturity. Over such a fragment and in the presence of dominant *S*, white-seeded varieties will have a brown spot on the seed coat.

However, many seed spots on Blackhull Kafirs and other varieties are caused by mechanical injury. Such damage is sometimes caused by sucking insects or diseases. When sorghum plants are damaged, any dead tissue becomes pigmented. The spots become blackish brown, reddish brown, or tan in color depending upon the genetic constitution of the plant with respect to the plant color genes *q* and *p*. Plants with black glumes have blackish brown spots, those with red glumes have reddish brown spots, and those with sienna or mahogany glumes have tan spots. Some strains of Pink Kafir have white seeds but reddish seed spots owing to the fact that the plant sap color is red. The reddish spots on the seed occur frequently enough to cause the seeds to have a pinkish cast.

Sorghum seed is frequently colored from being water-soaked during periods of rainy or damp weather as the seeds approach maturity. Color is taken into the outer seed layers either from the glumes or from the underlying brown testa. Seeds with a thick, chalky mesocarp are particularly subject to this kind of discoloration.

White-seeded varieties such as HEGARI and BONITA that have a brown testa frequently have brown seeds when killed by frost before maturity. It appears in this case that the cell walls of the immature seeds are ruptured from freezing and the brown pigment in the cells of the testa escapes into the mesocarp and epicarp.

b. Glume Color. The glumes that inclose the grain are green because of their chlorophyll content until the plant approaches maturity, at which time they assume colors that are determined by the genetic constitution of the plant. The glume colors are various shades of straw, red, black, sienna, or mahogany.

Red and black glume colors are the expression of alleles. Red is dominant to black in some varieties and recessive in others. The simplest explanation of this condition is an allelic series at the glume color locus, and Stephens (1947) has proposed that the allele for recessive red be designated q^r. In this scheme, the designation for dominant red is Q and for black, q. The designation of Qq was made by Ayyangar *et al.* (1933a).

There are two plant colors, purple and brown, and the designation Pp has been assigned to the factor pair by Ayyangar *et al.* (1933a). Plants with dominant P are either reddish or blackish purple depending on the genetic constitution for the Q gene. Plants with recessive p are brown or tan, and this brown plant color modifies the red and black colors caused by the factor pair Qq. Modified black plants have mahogany-colored glumes, and modified red plants have sienna-colored glumes. The genes Q and P are on different chromosomes. There are glume colors in Broomcorn that are neither red, black, mahogany, nor sienna. Stephens, in work that is unpublished, found that the gene that produces the glume colors of CALIFORNIA GOLDEN and BLACK SPANISH BROOMCORNS is independent of the gene Q in inheritance and its linkage relations with the midrib gene, Dd. indicate that it is an allele of p. The allele does not cause tan plant color, as does recessive p, but it does modify the stalk color somewhat just as it modifies the glume color.

A number of sorghum varieties have straw-colored glumes. A recessive dilution factor and a dominant glume color inhibitor have been reported and there is unpublished evidence at Chillicothe that one factor for straw glumes may be located on the q b gs chromosome. It appears that plants that are recessive for b_1 or b_2 and have no brown testa in the seeds have a tendency to have glumes that fade to straw color under adverse growing conditions. At Chillicothe, there is so much variation in the straw glumed character that it has not been possible to tell if the inhibitor that causes straw glumes is an allele of Q or B or whether it is another gene on the same chromosome. The recessive dilution factor cd reported by Ayyangar and Ponnaiya (1941) is independent of the gene Q. The dominant color inhibitor Ci of Ayyangar and Ponnaiya was not tested in populations segregating for the factor pair Qq. Probably the allele Ci, since it is dominant, is not one of the factor pair that segregates in populations of Blackhull Kafir and Feterita parentage. It appears, therefore, that there are at least two and probably three genes that produce straw glumes.

The plant color gene Y that produces color in dead plant tissue and in the pericarp of the seed has an influence on glume color. The total effect of the factor pairs Yy, Qq, Pp, the modifier in Broomcorn, and the color inhibitors that cause the glumes to fade to straw, is to produce a range in glume color from straw to blackish purple, reddish purple, golden, mahogany, and sienna.

c. Juiciness and Sweetness of Stalk. Sorghum stalks are pithy or juicy and sweet or nonsweet. The factor pair *Dd* controls the juiciness of the stalk and, according to Hilson (1916), pithy is a simple dominant to juicy. According to Ayyangar (1935), 17 to 20 per cent of juice can be extracted from pithy stalked varieties and 33 to 48 per cent from juicy varieties. Pithy stalked plants have white leaf midribs and juicy stalked plants, opaque midribs.

The inheritance of sweet and nonsweet stalks was studied by Ayyangar *et al.* (1936a) and they found nonsweet to be a simple dominant to sweet and assigned the symbols *Xx* to the factor pair. These authors also reported genes *X* and *D* to be independent in inheritance.

Swanson and Parker (1931) studied the association of juiciness and sweetness with kernel smut of sorghum and found that it was sweetness more than juiciness that was correlated with the susceptibility of a variety. However, SPUR FETERITA is sweet but pithy and is resistant to all races of the kernel smuts, *Sphaeclotheca sorgi* (Lk.) Cl. and *S. cruneta* (Kuhn) Potter, as reported by Melchers (1940). Apparently susceptibility or resistance to these fungi is controlled by factors other than those controlling juiciness and sweetness.

d. Height. Sorghum varieties range in height from 2 to 15 ft. Tall varieties are preferred for forage, because fodder yields are almost proportional to plant height. Except in the United States and Australia, dwarfness is not now considered advantageous, even in grain varieties, because the stalks are needed for fodder or building purposes. However, dwarf strains of Kafir, Durra, Hegari, Kaoliang, and Broomcorn have come to America from Africa, Asia, or Europe. Several mutations to dwarfness have occurred in this country since sorghums were introduced, and fully 95 per cent of the sorghum grain produced in the United States now is grown on short-stalked varieties that are harvested with a combine. These short varieties, except for DOUBLE DWARF MILO 38, resulted from combining dwarfness from more than one source.

Laubscher (1945) studied sorghum populations that were segregating for height, and concluded from F_2 data that the inheritance was complex. Since his populations were segregating for duration of growth and he did not study any F_3 populations, there is reason to question the accuracy of his conclusion. Two genes for dwarfness have been reported in Milo by Karper (1932) and in Broomcorn by Sieglinger (1932). It has recently been determined by Quinby and Karper (1954) that there are four recessive genes and a modifying complex that reduce internode elongation in sorghum. These genes have no visible manifestations other than shortening the internodes, since leaf number and size and time of blooming are the same in strains of the same variety of different heights. Genes that influence duration of growth also influence height through number of internodes, but these genes are more properly considered to be "maturity" genes.

Sixteen genotypes result from the independent assortment of four recessive genes. Ten of these genotypes were recognized among the common varieties. The genetic identity of certain varieties is shown in Table III. It will be seen that no variety was found to be dominant for all four genes and none recessive for all four. The tall MILOS, SPUR FETERITA, SHALLU, SUMAC, and DURRA are recessive for dw_1; and STANDARD BROOMCORN is recessive for dw_3. Recessive dw_4 is common to all the MILOS, TEXAS BLACKHULL KAFIR, SPUR FETERITA, the HEGARIS, SUMAC, and all Milo, Kafir, and Hegari hybrid selections. Dominance for Dw_4 is the peculiarity of the Broomcorns. Most of the forage sorghums are apparently recessive for one gene. The dual-purpose sorghums that are used for both grain and forage or were formerly grown

TABLE III

Classification of Sorghum Varieties According to Height

Genotype	Variety
Dw_1 Dw_2 Dw_3 Dw_4	None identified
Dw_1 Dw_2 Dw_3 dw_4	DURRA PI 54484, TALL WHITE SOONER MILO SA 1170, SPUR FETERITA, SHALLU Agros. 2650, SUMAC
Dw_1 Dw_2 dw_3 Dw_4	STANDARD BROOMCORN
Dw_1 dw_2 Dw_3 Dw_4	None identified
dw_1 Dw_2 Dw_3 Dw_4	None identified
Dw_1 Dw_2 dw_3 dw_4	TEXAS BLACKHULL KAFIR, KALO, EARLY KALO, CHILTEX
Dw_1 dw_2 Dw_3 dw_4	BONITA, HEGARI, EARLY HEGARI
dw_1 Dw_2 Dw_3 dw_4	DWARF YELLOW and WHITE MILOS, SOONER MILO
Dw_1 dw_2 dw_3 Dw_4	ACME BROOMCORN
dw_1 Dw_2 dw_3 Dw_4	JAPANESE DWARF BROOMCORN
dw_1 dw_2 Dw_3 Dw_4	None identified
Dw_1 dw_2 dw_3 dw_4	None identified
dw_1 Dw_2 dw_3 dw_4	PLAINSMAN, MARTIN, WHEATLAND, DAY, WESTLAND, MIDLAND, COMBINE KAFIR 60, the REDBINES
dw_1 dw_2 Dw_3 dw_4	DOUBLE DWARF YELLOW MILO, DOUBLE DWARF YELLOW and WHITE SOONER MILOS
dw_1 dw_2 dw_3 Dw_4	None identified
dw_1 dw_2 dw_3 dw_4	No commercial varieties

for hand heading, such as BLACKHULL KAFIR, HEGARI, and DWARF MILO, are recessive for two genes. The varieties used now for combine harvesting, such as COMBINE KAFIR 60, the REDBINES, PLAINSMAN, WESTLAND, MARTIN, and MIDLAND, are recessive for the three genes, dw_1, dw_3, and dw_4.

The recessive condition of a single gene shortens a variety by 30 cm. or more. At Chillicothe, strains recessive for three genes are frequently about 50 cm. to the upper leaf; those recessive for two genes, 100 cm.; and those recessive for one gene, 150 cm. or more. The modifying complex shortens height by about as much as a single recessive gene. Varieties that have the modifying complex that shortens stature are SPUR FETERITA, all of the MILOS, TEXAS BLACKHULL KAFIR, BONITA, the HEGARIS, and PLAINSMAN. MARTIN and PLAINSMAN presumably differ in modifying complex, as MARTIN was 9 cm. taller than PLAINSMAN at Chillicothe in 1949.

At least one of these height genes is unstable in some strains. There is an unstable gene in Kafir, studied by Karper (1932), that reverts to the dominant condition once in 1200 gametes. This unstable condition is a continual source of trouble to seed growers, because the resulting tall plants must be rogued from the seed fields, after which 10 or 20 tall plants per acre may still appear in farmers' fields owing to reversions. All of the short-stalked varieties of Kafir parentage such as MARTIN, PLAINSMAN, the REDBINES, COMBINE KAFIR 60, WESTLAND, and MIDLAND have this unstable gene in the recessive condition. EARLY HEGARI also has an unstable gene. TEXAS BLACKHULL KAFIR is recessive for dw_3 and dw_4. The unstable gene must be one or both of these two. Tall plants have not been seen in fields of BONITA or HEGARI that are genetically identical to EARLY HEGARI in height genes. Neither have tall plants ever been seen in fields of the Milo strains.

e. Duration of Growth. In a plant with a terminal inflorescence such as sorghum, duration of growth and ultimate plant size are dependent upon the time at which floral initiation takes place. A delay in the initiation of a floral bud results in a thicker stem and a larger number of nodes, internodes, and leaves, bringing about a delay in flowering and maturity.

Sorghum is a short-day species, since maturity is hastened by shorter days. Varieties differ in their responsiveness to day length. All of the strains of Milo are sensitive to a short photoperiod and cannot be distinguished from one another under 10-hour days. The Milo strains of different maturity apparently differ from one another in critical photoperiod or differ in the length of day under which they will initiate a head.

Many varieties other than Milo are photoperiodically sensitive, but other sorghum varieties are insensitive to photoperiod or exhibit varying degrees of sensitivity. Sorghum varieties were subjected to 10-hour and normal photoperiods during two summers at Chillicothe, Texas, by Quinby and Karper (1947) with similar results each year. The data obtained from the 12 varieties grown in 1941 are presented in Table IV. The data show that the list of sensitive varieties includes both MILOS, HEGARI, KALO, CALIFORNIA WHITE DURRA, SPUR FETERITA, and FREED. MANKO is a little less sensitive than this group but more sensitive than BISHOP, SUMAC, and BLACKHULL KAFIR. DWARF BROOMCORN alone was insensitive to the effect of 10-hour days. Sensitivity to photoperiod is inherited as a dominant. It can be inferred from work with other species that the thermal requirements have not been met if a sorghum variety is not sensitive to photoperiod. Likewise it can be inferred that varying degrees of sensitivity indicate that the thermal requirements have been partially met.

TABLE IV

Effect of 10-Hour Photoperiod on Time of Floral Initiation, Leaf Number, and Time of Anthesis of Sorghum Varieties Planted July 13, 1941, at Chillicothe, Texas

Serial No.	Variety	Number of days from planting to:				Number of leaves on mature plant	
		Head differentiation		First anthesis			
		Short * day	Normal day	Short day	Normal day	Short day	Normal day
SA 5043	SOONER MILO	23	32	43	49	11	13
TS 25243-276	TEXAS MILO	23	39	47	68	11	18
SPI 34911	HEGARI	23	48	47	77	13	18
FC 16207	KALO	23	39	47	64	11	17
SA 208	CALIFORNIA WHITE DURRA	23	34	51	55	13	14
FC 6601	SPUR FETERITA	23	36	56	65	16	19
SPI 29166	FREED	23	32	46	51	10	12
FC 8991	MANKO	25	47	50	77	12	17
FC 8993	BISHOP	28	39	61	71	14	17
SPI 35038	SUMAC	29	39	60	65	14	16
FC 6607	BLACKHULL KAFIR	29	39	59	69	14	16
SPI 30204	DWARF BROOMCORN	39	39	68	68	15	15

* Short day exposure to sunlight was 10 hours. In July at Chillicothe, Texas, the sun is above the horizon for about 14 hours.

The difference in maturity between SOONER MILO and TEXAS MILO, EARLY HEGARI and HEGARI, EARLY KALO and KALO is due to the different critical photoperiod of the early- and late-maturing strains. The differences in critical photoperiod within a group are caused by a few genes, and it is relatively simple to determine how many genes are involved. This has been done for the MILOS, HEGARIS, and KALOS. When photoperiodically sensitive and insensitive varieties are involved in crosses, however, the situation is more complex. The inheritance of maturity within an insensitive group such as the Broomcorns has not yet been studied.

EARLY HEGARI and HEGARI differ by a single allele. Lateness is partially dominant to earliness. EARLY KALO and KALO differ in a single allele, but, in this case, earliness is partially dominant.

Quinby and Karper (1945) found that in Milo three genes influence time of maturity. The independent assortment of these three genes results in eight homozygous genotypes but only four phenotypes. The genetic constitution of these eight genotypes and their times of anthesis are shown in Table V. The early, intermediate, and late phenotypes are varieties that are or were grown by farmers. The early phenotype includes all of the SOONER MILOS, the intermediate phenotype includes TEXAS MILO and DOUBLE DWARF MILO NO. 38, and the late phenotype was at one time grown under the name of DESERT MILO. The GIANT MILO that became extinct about 50 years ago was presumably a tall, ultralate strain. There is a linkage between the white pericarp color gene, *y*, and the maturity gene, Ma_3. There is also a linkage between the maturity gene, Ma_1, and the height gene, dw_2. The DOUBLE DWARF

TABLE V

A Tabulation of Genotypes and Phenotypes of Milo and Their Times of Blooming

Genotype	Phenotype	Days from planting to anthesis*
$Ma\ Ma_2\ Ma_3$	Ultralate	92–106
$Ma\ Ma_2\ ma_3$	Ultralate	92–106
$Ma\ ma_2\ Ma_3$	Late	76–88
$ma\ Ma_2\ Ma_3$	Early	46–60
$Ma\ ma_2\ ma_3$	Intermediate	64–74
$ma\ Ma_2\ ma_3$	Early	46–60
$ma\ ma_2\ Ma_3$	Early	46–60
$ma\ ma_2\ ma_3$	Early	46–60

* At Chillicothe, Texas.

SOONER MILOS were selected from a cross between TALL WHITE SOONER MILO and DOUBLE DWARF YELLOW MILO. The linkage between ma_1 and Dw_2 had to be broken before Sooner Milos of the double dwarf height could be obtained.

f. Callus Formation and Seed Shedding. Several mechanisms are involved in seed shedding in sorghum. The amount of shedding of seeds from the inclosing glumes varies with the length of the glumes and whether or not the glumes are involute. Spikelets are shed because of breaking of the pedicels or abscission at a callus. All of the methods of shedding except the last are quantitative characters. The inheritance of the quantitative characters has not been determined. However, abscission at a callus depends only upon whether a callus is or is not formed. The inheritance of callus formation has been determined.

Callus formation and abscission of spikelets is a characteristic of some of the grassy relatives of common sorghum, including Johnson grass. Sudan grass does not produce an abscission layer, and spikelets are shed only when the pedicels break. The wild relatives of sorghum that have 10 pairs of chromosomes cross readily with common sorghum and Sudan grass.

Ayyangar *et al.* (1936c) studied the offspring of a natural hybrid that shed its seed at the callus, and found seed shedding due to callus formation to be a simple recessive in inheritance. The designation Sh_1 was applied to this gene. Karper and Quinby (1947a), working with hybrids between Tunis grass and Sudan grass and several sorghum varieties, found callus formation and seed shedding to be dominant to nonshedding rather than recessive. F_1 plants invariably formed abscission layers and shed their seed. TEXAS BLACKHULL KAFIR, HONEY, and Sudan grass were found to differ from Tunis grass in one allele, but the LEOTI variety differed by two alleles, both of which needed to be present in the dominant condition before a callus formed. The designations Sh_2 and Sh_3 were assigned to these two genes, but it is quite possible that either Sh_2 or Sh_3 may be found to be identical to Sh_1 in spite of the reversal of dominance.

g. Endosperm Characters. Several endosperm characters of importance in sorghum are counterparts of the same characters in maize, *Zea mays*, L.

(*1*) *Yellow.* Several varieties with yellow endosperm were brought into the United States from Nigeria in 1952 by Dr. O. J. Webster of the United States Department of Agriculture and the Nebraska Agricultural Experiment Station. These varieties had not previously been introduced into the United States. SNOWDEN (1936) classified these varieties as *Sorghum caudatum* var. HACWELLI and reported that the flour made from the variety KERISTINGIANUM was decidedly yellowish in color without mentioning that the pigment came from the endosperm. The yellow pigment contains Vitamin A and is undoubtedly similar to the yellow endosperm of maize. The inheritance of this yellow endosperm character has not been reported as yet. This yellow endosperm color is now being incorporated into adapted varieties at several experiment stations.

(2) *Waxy*. There are two kinds of starch found in varieties of many cereals, including rice, maize, millet, coix, barley, and sorghum. Waxy starch, which stains red with iodine, is amylopectin, a branched glucose polymer, and is composed only of this one type of molecule. Common starch that stains blue with iodine is a mixture of amylopectin along with an unbranched or linear polymer, amylose. The properties of waxy starch make it of particular interest to industry, as it forms a clear paste which has little tendency to gel on standing. During World War II, waxy sorghum was made into a dessert that resembles tapioca. Extensive studies of the chemical properties of sorghum grain and of the properties of sorghum starch have been made by Barham *et al.* (1946).

Waxy endosperm of sorghum was first reported by Meyer (1886). Karper (1933) found waxy to be a simple recessive to starchy in segregating populations. Adapted sorghum varieties with the waxy type of starch have been produced and can be increased rapidly whenever there is a demand for this type of starch.

(3) *Sugary*. There is a sugary endosperm character in sorghum similar to that in maize. The character occurs in a number of Indian varieties and a sugary mutation was found at Chillicothe, Texas, in a BLACKHULL KAFIR × SUMAC cross in 1934. Karper *et al.* (1934) and Ayyangar *et al.* (1936b) studied the inheritance of a sugary gene in sorghum and found that sugary is a simple recessive. In 1938, J. C. Stephens, in work that is yet unreported, intercrossed three sugary strains; the F_1 in each case was sugary, indicating that the same sugary gene was common to all three strains. The three strains used in the crosses were the BLACKHULL KAFIR × SUMAC mutation mentioned above, an Indian variety, VANI, introduced by R. E. Karper in 1933, and KACHADACHI, P. I. 14746, introduced by the United States Department of Agriculture from Bombay Presidency, India, in 1903 but first grown at Chillicothe in 1933 from seed picked from a herbarium head in the collection of H. N. Vinall.

The sugary varieties in India have "dimpled" grains. The sugary varieties from the Bellary district of the Madras Presidency are of three seed colors, white, yellow, or red. Young grains in the early milk stage begin to dimple. After about 15 days, the dimpling process is completed, and it is at this stage that the grains are most prized for eating. An analysis of sugary grains in India showed that the amount of reducing sugars in the dimpled grains is three times the quantity found in the nondimpled grains, the nonreducing sugars being equal in both. No commercial use has been made of this character in the United States. In India, sugary grain sorghum is parched by placing green heads in beds of coals. The grain is then knocked from the heads and eaten.

(*4*) *Floury.* A number of Kaoliangs from Manchuria have a floury type of starch in the endosperm. It has never been possible to separate floury from nonfloury seeds on segregating heads, but the character is evidently a counterpart of that of varieties of maize.

(5) *Pop sorghum.* Popping varieties of sorghum are grown in India, and pop sorghum is eaten there just as popcorn is eaten in America. The popping varieties according to Ayyangar and Ayyar (1936) are characterized by small grains with a hard endosperm which is very dense. The seed coats of the popping varieties are comparatively thick. The expansion ratios of Indian varieties are sometimes as high as 15 or 17 to 1. The type of endosperm that causes high expansion ratios has been transferred to strains adapted in the United States by R. E. Karper. One variety, called POP SORGHUM, which has PETIT MIL, a Haitian variety, and SHALLU in its parentage, has been distributed by the Texas Agricultural Experiment Station, but there has been no commercial production. In the present varieties, the expansion ratio does not compare favorably with that of the best popcorns, but expansions up to 32 to 1 have been obtained with special techniques. Pop sorghum makes a smaller popped kernel than popcorn, but it is more tender, has less hull, does not clog the spaces between the teeth, and causes less noise when eaten. The smaller puffs lie closer together and weigh more per unit of volume than pop corn and are just as flavorful and nutritious. In areas where sorghum is adapted, pop sorghum has value as a substitute for popcorn. Its value in commercial fields awaits further exploration and development, but there should be possibilities and opportunities for its use in caramel and candied confections, for puffed breakfast cereals, for flour and meal, and in the packing of fragile articles for air transport.

h. Milo Disease Resistance. Extensive lists of varieties resistant or susceptible to Milo disease, caused by *Periconia circinata* (Mong) Sacc., have been published by Wagner (1936) and Melchers and Lowe (1940). Bowman *et al.* (1937) found susceptibility to Milo disease to be partially dominant in inheritance.

i. Resistance to Charcoal Rot. A destructive stalk rot of sorghum, caused by the fungus *Macrophomina phaseoli* (Maubl.) Ashby, is called Charcoal rot. The disease causes severe lodging, because the culms break over close to the ground level when the pith of the lower internodes rots away. Attack by the fungus *Fusarium moniliforme* Sheldon produces symptoms that are sometimes quite similar to those produced by *M. phaseoli,* and there is a tendency to attribute the damage to Charcoal rot regardless of which fungus is responsible. Leukel *et al.* (1951) have described the symptoms and published photographs showing damage from these diseases. Tullis (1951) reported on work done with *F. moniliforme* and cited the pertinent literature.

There is resistance to both of these diseases in sorghum, but the expression of susceptibility is variable in the same field and from year to year. Tullis (1951) found resistance to *F. moniliforme* in TEXAS BLACKHULL KAFIR, FETERITA FC 811, and EXTRA EARLY SUMAC. No variety is considered to be immune to attack from these fungi.

The expression of resistance or susceptibility is so variable that it has not been possible to determine the mode of inheritance of resistance to these stalk-rotting fungi.

j. Resistance to Chinch Bugs. The chinch bug, *Blissus leucopterus* (Say). is a serious pest on sorghum in some parts of the sorghum belt in certain years. At Lawton, Oklahoma, the insect overwinters in great numbers on native grasses and migrates from small grain fields to sorghum by flying. In many areas, chinch bugs are troublesome when barley is grown, because the insects then have a specially favorable crop on which to increase. During the acreage control program of the Agricultural Adjustment Administration during the 1930's and early 1940's, barley was grown in some areas on retired wheat acreage with disastrous results to the sorghum crop. An effective breeding project for introduction of resistance of sorghum to the chinch bug was carried on by the Oklahoma Agricultural Experiment Station and the United States Department of Agriculture at Lawton, Oklahoma. A number of resistant strains that resulted from this work are being maintained as sources of chinch bug resistance if required later.

This breeding work and the studies of resistance to chinch bugs that went on at the same time gave some information of the inheritance of resistance. Snelling *et al.* (1937) reported on work at Manhattan, Kansas, and Lawton, Oklahoma, that showed that resistance was dominant, and that there was usually transgressive segregation for resistance, indicating that more than one gene was involved. Chinch bug resistance was not put on a definite genetic basis by this work, but there was ample evidence of its inheritance. Varieties of sorghum have been classified for susceptibility to damage from chinch bugs by a number of workers in several states, and this information has been summarized in a book by Painter (1951).

Dahms *et al.* (1936), working in Oklahoma, found that resistant varieties showed the greatest tolerance to a uniform infestation of chinch bugs, that the insects preferred susceptible varieties as hosts, that female chinch bugs lived longer on susceptible varieties than on resistant ones, that more eggs were laid on susceptible varieties, and that nymphs developed faster on susceptible varieties. This work is significant and shows that there is in plants actual resistance to insects produced by influencing the biology of the insect.

k. Linkage. Seven linkage groups have been reported in sorghum. Four of these groups have three or more genes and the other three involve only two genes. In several cases the linkage between two genes was reported before the plural linkages that follow were reported.

The linkage group *Q B Gs* was reported by Stephens and Quinby (1938). The contrasting phenotypes are reddish and blackish plant color that is shown conspicuously in the glumes, presence or absence of a brown testa, and normal green and striped plants. The factor pairs have the designations *Qq*, *Bb* and *Gsgs*, respectively. The order of genes with crossover percentages is *Q* (13.2) *B* (11.3) *Gs*. Ayyangar *et al.* (1934a) reported absolute linkage between the factor pairs *Qq* and either Bw_1 bw_1, or Bw_2 bw_2. These genes, which were erroneously designated B_1 and B_2 by Ayyangar *et al.* (1934b), in the dominant condition cause the presence of brown in the epicarp and dry anthers even in the absence of a testa that develops when both B_1 and B_2 are present in the dominant condition. Either Bw_1 or Bw_2 is therefore on the *Q B Gs* chromosome very close to the *Q* locus.

The linkage group *D Rs P* was reported by Stephens and Quinby (1939). The contrasting phenotypes are dry and juicy stalks, red and green seedling stem color, and purple and brown plant color. The factor pairs have the designations of *Dd*, *Rsrs*, and *Pp*, respectively. The indicated order of genes with crossover percentages is *D* (10.9) *Rs* (16.4) *P*. Karper (1930) reported a linkage between a gene for albino seedling color and the *Rs* gene with a crossing-over percentage of 41. This seedling abnormality has been lost.

The linkage group Ms_2 AV_{10} was reported by Stephens and Quinby (1945), and Stephens (1944) added Green Striped-2 to the group. The phenotypes are normal and male-sterile flowers, awnless and awned lemmas, green and virescent-yellow plants, and normal and green striped plants. The factor pairs have the designations Ms_2ms_2 *Aa*,

$V_{10}v_{10}$, and Gs_2gs_2, respectively. The order of genes with crossover percentages is Gs_2 (11.0) Ms_2 (10.9) A (9.1) V_{10}.

The Y V_{11} G_2 linkage group was reported by Stephens (1951). The phenotypes are red and white seed color, virescent yellow plant color, and green and golden plant color. The factor pairs have the designations Yy, $V_{11}v_{11}$ and G_2g_2, respectively. The order of genes with crossover percentages is Y (6.0) V_{11} (3.0) G_2. Quinby and Karper (1945) found a linkage between the gene that controls white or red pericarp color in Milo and the maturity gene Ma_3. The population observed was too small in number to allow an accurate estimate of crossover percentage, but ma_3 is evidently on the Y V_{11} G_2 chromosome and rather closely linked with Y.

Quinby and Karper (1945) reported a genetic linkage between the maturity gene Ma_1 and the internode elongation internode inhibitor dw_2. The populations that showed this linkage were too small in number to allow an accurate estimate of crossover percentage, but the figure is probably close to 8 per cent. Ayyangar *et al.* (1937) reported an association of tall height and late maturity, but in this case the association is apparently not genetic linkage, because the segregation was for duration of growth. Late-maturing plants had more internodes and were therefore taller.

A linkage between y_2, a yellow seedling deficiency, and the gene, wx, that produces waxy endosperm was reported by Karper *et al.* (1934). The crossover percentage between wx and y_2 was reported as being 26.5.

A linkage between a factor pair, loose head shape and compact head shape, and the factor pair that controls thickness of mesocarp has been reported by Ayyangar and Ayyar (1938). The genes were designated Pa_1pa_1 and Zz, and the crossover percentage between them was reported as being 1.07.

VII. Hybrid Vigor in Sorghum

1. *Common Sorghum*

First-generation sorghum hybrids are usually vigorous and are frequently late in maturity and tall in stature. The lateness and tallness are due to the complementary action of genes that affect time of floral initiation and of height. This complementary action of genes that affects duration of growth and height is sometimes confused with the type of heterosis that causes greater vigor of growth. This type of heterosis occurs in sorghum as in other species and results in plants that are somewhat larger, tiller more, and produce more grain and forage than pure varieties of comparable growth duration. Conner and Karper (1927), Karper and Quinby (1937), Bartel (1949), and Stephens and Quinby (1952) have described the magnitude of hybrid vigor in sorghum. Increases in size as great as three or four hundred per cent have been observed owing to a combination of complimentary action of height and maturity genes and growth vigor.

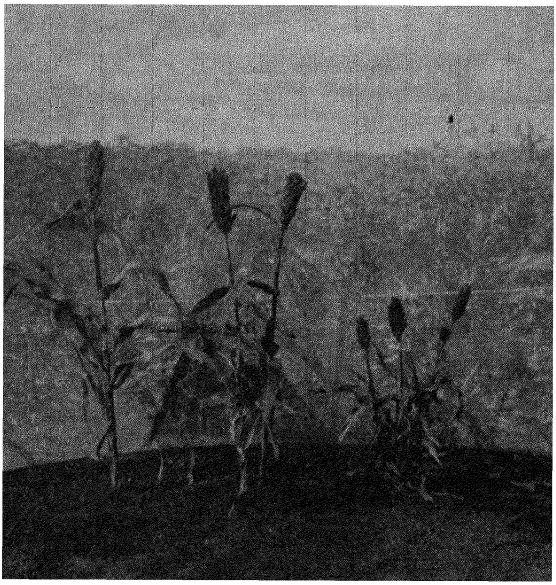

FIG. 5. An F_1 hybrid of Kafir × Day Milo between the Kafir parent on left and Day Milo parent on right. During 6 years in an April planting and 8 years in a June planting at Chillicothe, Texas, the F_1 produced 40% and 39% more grain, respectively, than Texas Blackhull Kafir, the highest producing parent.

a. Heterosis and Grain Production. An F_1 sorghum hybrid, TEXAS BLACKHULL KAFIR × DAY SELECTION, that has vigor without lateness of maturity or tall height, similar to the vigor of hybrid corn, was grown at the Chillicothe Station for six years in an April planting and for eight years in a June planting (Fig. 5). A summary of the results reported by Stephens and Quinby (1952) is shown in Table VI. The yield of the hybrid was 27 per cent above the average of all varieties in the April planting and 44 per cent above the average in the June planting. The hybrid variety yielded better than its appearance indicated because of a large number of grains per head, which is un-

TABLE VI

Average Yields, Days to Blooming, and Heights of a TEXAS BLACKHULL KAFIR X DAY SELECTION F_1 Hybrid and Locally Adapted Commercial Varieties at Texas Substation No. 12, Chillicothe, Texas

Entry	April 15 planting (Avg. 6 years)				June 15 planting (Avg. 8 years)			
	Grain yield		No. days to full bloom	Ht., in.	Grain yield		No. days to full bloom	Ht., in.
	Bu./acre	Per cent F_1 of variety			Bu./acre	Per cent F_1 of variety		
Hybrid:								
KAFIR X DAY F_1	42.6		75	49	44.6		59	42
Varieties:								
MARTIN	33.8	126	75	37	27.5	162	56	32
PLAINSMAN	33.6	127	78	34	30.6	146	56	30
CAPROCK	37.1	115	81	36	31.1	143	60	31
WESTLAND	29.3	145	77	36				
KALO	33.5	127	77	48	37.3	120	66	42
BONITA	38.9	110	76	46	36.9	121	62	39
TEXAS BLACKHULL KAFIR	30.5	140	79	52	32.2	139	66	48
SPUR FETERITA	32.4	131	79	54	29.4	152	62	53
CHILTEX	33.7	126	76	48	35.7	125	60	45
CODY	27.7	154	80	47				
AJAX	35.9	119	86	42	29.7	150	77	42
EARLY HEGARI	30.8	138	66	45	30.8	145	78	42
HEGARI	31.3	136	73	52	21.5	207	93	53
QUADROON	37.8	113	76	53				
MILO (chinch bug resistant)	32.0	133	74	47	33.3	134	73	45
TEXAS MILO	36.0	118	75	51	31.5	142	70	44
MAIZOLA	36.4	117	89	51	35.0	127	72	48
MANKO	35.3	121	98	60	22.6	197	91	53
DARSO 28	32.1	133	82	51	31.0	144	59	43
Average of varieties	33.6	127			31.0	144		

doubtedly an expression of hybrid vigor. This hybrid is not an ideal grain sorghum, but the data show what can be expected of hybrid sorghum in grain production.

b. Heterosis and Forage Production. There is interest in the hybrid vigor that is expressed in forage production as well as in grain production. Karper and Quinby (1937) have reported the yield of forage as well as grain of parent varieties and F_1 hybrids that were grown at Chillicothe, Texas. Of the several hybrids grown three had parents that did not have complementary genes for late maturity and tall height.

Part of the data from Karper and Quinby (1937) are presented in Table VII. The hybrids produced from 11 to 75 per cent more forage than the highest producing parent and had durations of growth as short as or shorter than either of the parents. In one case tillering was greatly above that of either parent, and, in the other two cases, tillering approached that of the highest tillering parent. Increases in forage production due to heterosis, exclusive of complementary action of maturity and height genes, appear to be as great as the increases in grain production.

TABLE VII

Height of Plant, Number of Stalks, Length of Growing Season, and Yield of Grain and Forage of Certain Varieties and Hybrids at Chillicothe, Texas, in 1932

Variety or hybrid	Height of plant, cm.	Stalks per plant	Growing season days	Yield per plant, lb.		Per cent increase over highest yielding parent	
				Forage	Grain	Forage	Grain
Parents:							
BLACKHULL KAFIR	126	1.0	105	0.64	0.20	—	—
SPUR FETERITA	157	1.3	100	0.81	0.26	—	—
SUMAC	187	2.1	100	1.21	0.26	—	—
RED KAFIR	128	1.0	105	0.59	0.13	—	—
Hybrids:							
BLACKHULL KAFIR × SUMAC	188	1.8	100	1.35*	0.41*	11	58
SPUR FETERITA × SUMAC	199	2.0	95	1.40*	0 54*	16	108
BLACKHULL KAFIR × RED KAFIR	135	1.7	105	1.12*	0.43*	75	115

* Significantly above yield of highest producing parent.

c. Causes of Heterosis in Sorghum. A number of theories have been advanced to account for heterosis, but there is no general agreement on this subject. Probably a number of different interactions play a part. The theories of dominant gene interaction, epistasis, and the interaction of alleles are three that have been advanced to account for heterosis. A little information about the manifestations of hybrid vigor, its cause, and the number of genes which may be involved has been developed in work with sorghum.

Quinby and Karper (1946), working within the Milo group of varieties, found that the heterozygous condition of the maturity gene Ma_1ma_1 caused lateness of maturity in some genotypes and earliness in others, and also caused larger heads and more tillering. It was concluded from this study that hybrid vigor in sorghum is shown in more rapid

TABLE VIII
The Effect of Different Alleles on Growth and Production of Sorghum Hybrids at Chillicothe, Texas, 1941

Parent or hybrid	Height, in.	Number of leaves	Number of stalks	Days to anthesis	Yield per plant, lb.		Yield of grain, bu./acre
					Grain	Stover	
Parents:							
TEXAS BLACKHULL KAFIR	37.3	13.1	1.2	63	0.19	0.24	21.8
SOONER MILO	36.3	9.3	2.5	58	0.21	0.27	24.0
TEXAS MILO	46.8	16.1	2.4	80	0.21	0.53	24.6
EARLY HEGARI	51.0	18.6	1.8	78	0.21	0.47	25.0
HEGARI	56.8	21.6	1.9	87	0.20	0.61	23.3
EARLY KALO	22.7	8.6	1.4	54	0.16	0.14	18.5
KALO	37.6	14.7	1.1	73	0.15	0.27	17.5
Hybrids:							
KAFIR × TEXAS MILO	99.2	19.9	2.2	96	0.38	0.92*	44.4
KAFIR × SOONER MILO	56.7	12.9	1.9	59	0.33	0.47	37.9
EARLY HEGARI × TEXAS MILO	87.0	21.1	2.1	95	0.32*	0.91	37.8
EARLY HEGARI × SOONER MILO	89.2	21.5	2.0	100	0.25	0.88	29.7
HEGARI × TEXAS MILO	90.9	20.9	1.8	94	0.50*	0.76	58.8
HEGARI × SOONER MILO	92.0	23.1	2.3	101	0.33	1.08*	38.7
HEGARI × TEXAS MILO	90.9	20.9	1.8	94	0.50*	0.76	58.8
EARLY HEGARI × TEXAS MILO	87.0	21.1	2.1	95	0.32	0.91*	37.8
KAFIR × EARLY HEGARI	98.7	20.0	1.9	98	0.27*	0.85	31.8
KAFIR × HEGARI	111.0	21.2	1.4	104	0.21	0.83	24.2
KAFIR × KALO	39.2	12.0	1.4	57	0.28*	0.28*	33.4
KAFIR × EARLY KALO	33.9	11.2	1.2	56	0.21	0.18	24.4

* Significantly different at the 0.01 level.

meristematic growth and more tillering. The period of meristematic growth starts with development of the embryo and continues until after head differentiation.

There are sorghum varieties that differ from one another only in one allele that affects maturity. Such pairs of varieties are TEXAS and SOONER MILOS, HEGARI and EARLY HEGARI, and KALO and EARLY KALO. TEXAS MILO and SOONER MILO differ in the first maturity gene. TEXAS MILO is dominant Ma_1 and SOONER MILO is recessive ma_1. HEGARI is dominant Ma_1, and EARLY HEGARI carries an allele, designated as Ma_1^e

that make it earlier in maturity than HEGARI. Both KALO and EARLY KALO are recessive ma_1, but EARLY KALO also carries a dominant gene for earliness. These pairs of varieties were crossed to a third variety and the F_1 plants were grown and observed for height, duration of growth, tillering, and yield of grain and stover. The data, reported by Quinby and Karper (1948), are shown in Table VIII.

All hybrids produced greater yields of grain and stover than the parents. Hybrids that differed in only one allele, in most cases, produced different yields of grain and stover. In several instances when EARLY HEGARI and HEGARI or EARLY KALO and KALO were the contrasting parents, the F_1 plants differed only slightly in duration of growth but differed significantly in grain production. It is apparent that the alleles that differentiate the Milo, Hegari, and Kalo pairs of varieties differ in combining ability. F_1 hybrids that differed from one another by only one allele and which had similar durations of growth produced grain yields that differed by 25 per cent or more. Since the Kafir × Kalo hybrid produced 33.4 bu. per acre and the Kafir × Early Kalo hybrid, 24.4 bu., the difference in combining ability between recessive ma_4 and dominant Ma_4 when crossed to Kafir is 9 bu. or 37 per cent. It will be noticed that in this case the recessive allele was the best "combiner." The allele Ma_1^e from EARLY HEGARI combined better with Kafir than did Ma_1 from HEGARI, but the opposite was the case in crosses with Milo. It is apparent from these results that one allele in sorghum can have a great influence on the combining ability of a strain.

2. *Sudan Grass*

It was reported from Australia by Wenholz (1934) that inbreeding Sudan grass reduced vigor. This is logical, since unselected Sudan grass is comprised of a heterogeneous mixture of different plant types. It has been reported by Garber and Atwood (1945) that cross-pollination in Sudan grass is frequently as high as 70 per cent. Cross-pollination in grain sorghums is much lower and is frequently only a few per cent. Since Sudan grass is more highly cross-pollinated than other sorghums, it is not surprising that vigor in this grass can be reduced by inbreeding.

In the process of selecting SWEET SUDAN grass from segregating populations, it was obvious that the sweet, juicy, sienna-glumed plants were less vigorous than the outcrosses that appeared in the same progeny rows. A sweet, juicy, sienna-glumed plant is recessive for at least four genes, and plants of that genotype that are selected in succeeding generations are likely to be due to self-pollination, even though there is no controlled pollination. Plants that are of any other phenotype than juicy and sienna, that appear in a progeny, the female parent of which was recessive for the *d*, *q*, and *p* genes, must be due to cross-pollination, and the offtype plants would of necessity be F_1 hybrids.

In 1942 at Chillicothe, Texas, the 52 plants that comprised the progeny of an open-pollinated plant that was homozygous recessive for juiciness, sweetness, and the two glume-color genes that produce sienna were harvested and weighed as they were cut. Twenty-one of the plants were sienna, sweet, and juicy, and thirty-one were dominant for at least one of the four genes. These 31 plants were due to outcrossing and were F_1 plants. The 21 plants were presumably due to self-pollination. The first-generation hybrid plants were 11 per cent taller, had 31 per cent more stalks per plant, and were 43 per cent heavier than the plants from self-pollinated seed that grew in the same row. The data are shown in Table IX. These data, although not extensive, are typical and indicate the possibilities that exist for increases in production when seed of hybrid Sudan grass is available. The *data* also indicate why it is difficult to obtain a vigorous strain when there is careful selection for any one character, whether it be glume color, juiciness, sweetness, or low prussic acid content.

TABLE IX

Height, Number of Stalks, and Green Weight of Selfed and Cross-Pollinated Plants of SWEET SUDAN Grass. Data from Chillicothe, Texas, 1942

	Height, in.	No. of stalks	Green plant weight, lb.
Self-pollinated plants	84 0 ± 1 8	7 5 ± .02	1.03 ± .07
Outcrossed plants	93 3 ± 1 3	9 8 ± 57	1.47 ± .28
Per cent increase	11	31	43

VIII. Progress in Production of Hybrid Sorghum

1. *Early Work with Male Steriles*

Work to devise methods for producing hybrid sorghum seed in quantity has been underway at the Texas Agricultural Experiment Station in co-operation with the United States Department of Agriculture for more than 20 years. In 1929, J. C. Stephens discovered an antherless character in Sudan grass, and this abnormality was reported by Karper and Stephens (1936). This abnormality was worked with for several years, but, in 1935, Stephens discovered a genetic male-sterile character in TEXAS BLACKHULL KAFIR, and it was obvious from the start that this was a still better male-sterile than the one found in

Sudan grass. A male-sterile was reported from India about the same time by Ayyangar and Ponnaiya (1936). Stephens (1937) designated the character found in India, ms_1 and that found in Kafir, ms_2. The ms_2 in Kafir was apparently partially female-sterile also, and, in the original stock, open-pollinated heads produced seed in only 10 or 15 per cent of the florets. After several years of work, there were strains of the ms_2 stock that produced good sets of seed when open-pollinated, and it was proposed by Stephens (1937) that this male-sterile might be used for the production of hybrid sorghum seed. By 1946 work with ms_2 had progressed to the point when it appeared that hybrid sorghum might be put into production. However, in 1943 a still better male-sterile was discovered by Glen H. Kuykendall in a field of the DAY variety on his father's farm near Cookeville, Tennessee. Kuykendall sent several F_1 DAY male-sterile strains to the Chillicothe Station for observation in 1947.

2. *The* DAY *Male-Sterile*

This DAY male-sterile proved to be a genetic male-sterile that when crossed to some varieties gave F_1 plants that were sterile or partially so, and when crossed to other varieties gave F_1 plants that were fertile. After several years of work with the DAY male-sterile, it was apparent that the variety could be used for the production of hybrid sorghum, even though complete male-sterility had not been attained. The proposed procedure for the production of hybrid seed by a three-way cross was published by Stephens *et al.* (1952). Kuykendall, who discovered this DAY male-sterile, worked for the Texas Agricultural Experiment Station for one year, but in 1949 was employed by the DeKalb Hybrid Seed Company and has been doing breeding work with this male-sterile near Littlefield, Texas. DAY male-sterile stock was distributed to other sorghum plant breeders by the Texas Agricultural Experiment Station in 1951.

3. *The Cytoplasmic Male-Sterile*

During the time that partial fertility was being reduced in the DAY male-sterile stock, Stephens was trying to determine the inheritance of the male-sterile character. In this work, reciprocal crosses were made between SOONER MILO and TEXAS BLACKHULL KAFIR. F_1 plants were grown in 1949, and the following year partial male-sterility was found in F_2 populations of those crosses having Milo as the female parent. Holland (1952) reported the early data from this study in a thesis. It soon became apparent that male-sterility in this case was due to interaction between Milo cytoplasm and Kafir nuclear factors, as reported by Stephens and Holland (1954). The results indicate that the degree of sterility is increased as the proportion of Kafir chromosomes in Milo cytoplasm is increased. The number of genes involved has not been estimated accurately as yet, because the occurrence of sterility caused by unfavorable environment during the 1952 and 1953 seasons at Chillicothe confused the expression of genetic sterility.

The cytoplasmic type of male-sterility has advantages over the three-way cross for the production of hybrid seed. At the present time, cytoplasmic male-sterile stocks that have been backcrossed to Kafir four times are in existence. Some of these strains are completely or nearly sterile, and several strains are apparently suitable as seed parents for commercial crosses. Pollen-restoring strains have been found, and it is not anticipated that there will be any great difficulty in finding suitable pollen parents.

The genetic DAY male-sterile is in Milo cytoplasm, and it is possible to produce a cytoplasmic male-sterile strain without any emasculation by using the genetic male-sterile DAY as a female parent and backcrossing to Kafir several times. The genetic male-sterile, and the susceptibility of the DAY variety to Milo disease, Charcoal rot, weak-neck, and chinch bugs as well, would ultimately be eliminated by this process. This procedure has been followed by N. W. Kramer of the Texas Agricultural Experiment Station, O. J. Webster of the Nebraska, and E. G. Heyne of the Kansas Agricultural Experiment Stations and the United States Department of Agriculture, and all have obtained satisfactory cytoplasmic male-sterile seed parents. Mr. J. B. Sieglinger of the Oklahoma Agricultural Experiment Station and the United States Department of Agriculture has produced a male-sterile originating in material with no DAY male-sterile in its parentage that appears to be cytoplasmic in inheritance.

It has already been established by Stephens and Holland at Chillicothe, Texas (unpublished data), that cross-pollination in sorghum is effective over at least twelve 40-inch rows. Satisfactory male-sterile seed parents are already in existence, and suitable pollen-restoring male parents will undoubtedly be found among the hundreds of strains already in existence. A particularly large collection of strains that originated in the sorghum breeding work is being maintained by R. E. Karper at the Lubbock Station. A considerable number of derived strains are also at Chillicothe, the result of work by J. C. Stephens. There appears to be no serious hindrance in the hybrid seed production procedure, but it is realized that trouble may arise in unanticipated places. From the hybrid seed producers' standpoint, the greatest uncertainty will be in getting simultaneous blooming of seed and pollen parents.

4. Maintenance of Parental Stocks and Production of Hybrid Seed

Before hybrid sorghum can be grown by farmers, hybrid sorghum seed must be produced by seed growers. To make it clear how hybrid seed will be produced, it might be well to follow the method of production through all the steps from maintenance of parental stocks to production in farmers' fields. The necessary steps for maintaining stocks and producing hybrid seed are shown in Fig. 6, prepared by J. C. Stephens.

Male-sterile strain A will be produced in a crossing block in which the pollen parent is Normal strain A. Hybrid sorghum seed will be produced in a second crossing block in which the seed parent rows will be Male-sterile strain A and the pollen parent will be Normal strain B, a male-fertile restoring strain. The seed produced in the second crossing block will be planted by sorghum growers for commercial production.

It will be seen from this brief explanation that the seed parent in both maintenance and seed-grower crossing blocks will be Male-sterile strain A. Male-sterile strain A is a counterpart of Normal strain A, but the former has Milo cytoplasm and the latter, Kafir cytoplasm. The chromosome complement of both strains will be the same, because Male-sterile strain A is maintained by backcrossing to Normal strain A. Male-sterile strain A and Normal strain A will look alike, but one will, and the other will not, produce grain if the heads are bagged. Normal strain A will be a fertile strain, and a seed supply will be maintained by harvesting seed from the pollen rows of the maintenance crossing block. Normal strain B will also be a fertile strain, which could be maintained by harvesting seed from the pollen parent rows in the seed-grower crossing blocks.

It is estimated that one-quarter acre of land will be necessary to increase seed of Male-sterile strain A for every 100 acres planted to seed rows in seed-grower crossing blocks. Assuming that ten thousand acres will ultimately be planted to seed-grower crossing blocks, it would be necessary to plant 25 acres of the maintenance crossing block. It is possible that many commercial seed growers would prefer to purchase seed of Male-sterile strain A rather than produce their own supply and, in such a case, experiment stations or crop improvement associations might well produce the seed of Male-sterile strain A.

The production of hybrid sorghum seed with the use of cytoplasmic male-sterility is a simple procedure. After the production problems that are sure to arise have been overcome, the cost of producing hybrid sorghum will not be greatly in excess of the present cost of producing certified seed. It is not known at present what the best practices will be in the production of hybrid sorghum seed. The number of rows of the male-sterile seed parent that will be planted between rows of the pollen parent will depend not only on the dispersal of pollen but upon the kind of equipment available, and on the ease of planting and of combining at harvest. Probably the first seed growers will plant two rows of the pollen parent to four rows of the seed parent, but other combinations may prove to be more suitable. If simultaneous blooming of seed and

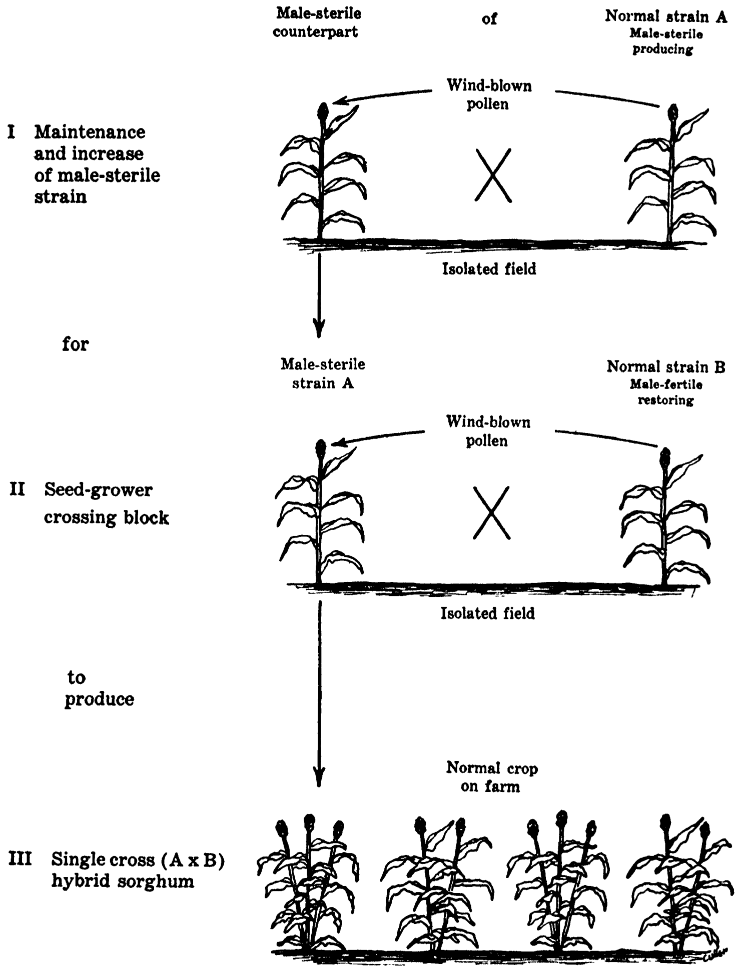

FIG. 6. Diagram showing the method of maintaining seed of a cytoplasmic male-sterile seed parent and of producing hybrid sorghum seed.

pollen parents in seed-grower crossing blocks is a problem with some crosses, it may be necessary to plant the two parents at different times or to devise methods to lengthen the time of pollen shedding. Suitable production practices will undoubtedly develop as seed growers start and expand production.

There has already been preliminary testing of sorghum hybrids produced by the three-way cross by the DeKalb Hybrid Seed Company. Hybrids produced on cytoplasmic male-sterile plants were tested at Texas Agricultural Experiment Stations in 1954 and soon it should be possible to recognize some suitable hybrids so that parental seed stocks can be put in the hands of seed growers. Hybrid sorghum seed that is produced by use of the cytoplasmic male-sterile will be from a single cross. In all probability the first hybrid that is distributed will have a Combine Kafir as a seed parent and some red-seeded combine type similar to REDBINE 60 as a pollen parent. Such hybrid seed will be white, but the crop grown from that seed will be red. Obviously, some educational work will need to be done to explain this matter at the time when the first hybrid seed is sold.

5. *Hybrid Sorghum for Forage Production*

There are possibilities of using sorghum hybrids to produce increases in forage yield as well as grain yield and to increase the supply of sorgo seed. In this day of mechanization, there is almost invariably a shortage of forage sorghum and Sudan grass seed. At the present time, seed of the forage and syrup sorghums and Sudan grass is produced by growing plants in rows, harvesting with a row binder, shocking, and then threshing from the shocks. This is a labor-consuming process, and the amount of work involved has discouraged seed production. Hybrid sorghum affords a way of producing sorgo and Sudan grass seed at little additional expense over that involved in producing a crop of grain. It should be possible to produce male-sterile seed parents that are both sweet and juicy and that can be combined as grain crops are. A tall growing sorgo could be used as the male parent of the cross, and the resulting hybrid would not only be vigorous but would be tall in the farmer's field. If lack of seed production would be an advantage in a forage or silage crop, a sterile producing strain could be used as the pollen parent. The seed that would be produced in the seed growers field would grow on short-stalked plants, and the seed would be harvested with a combine. The same procedure could be used in the production of hybrid Sudan grass. It is believed that hybrid Sudan grass is the answer to the problem of inbreeding which reduces vigor in this crop. Parental strains for the production of several hybrid grain varieties are already in existence, but most of the breeding work to produce forage and grass sorghum hybrids still remains to be done.

REFERENCES

Artschwager, Ernst. 1948. *U. S. Dept. Agr. Tech. Bull.* **957.**

Artschwager, Ernst, and McGuire, Ruth C. 1949. *J. Agr. Research* **78,** 659–673.

Ayyangar, G. N. R. 1935. *Madras Agr. J.* **23,** 350–352.

Ayyangar, G. N. R., and Ayyar, M. A. S. 1936. *Madras Agr. J.* **24,** 323–328.

Ayyangar, G. N. R., and Ayyar, M. A. S. 1938. *Proc. Indian Acad. Sci.* **8,** Sec. B 100–107.

Ayyangar, G. N. R., and Krishnaswami, N. 1941. *Proc. Indian Acad. Sci.* **14,** Sec. B 114–136.

Ayyangar, G. N. R., and Nambiar, A. K. 1938. *Madras Agr. J.* **26,** 465–468.

Ayyangar, G. N. R., and Ponnaiya, B. W. X. 1936. *Current Sci. (India)* **5,** 390.

Ayyangar, G. N. R., and Ponnaiya, B. W. X. 1941. *Current Sci. (India)* **10,** 410–411.

Ayyangar, G. N. R., Vijianaghavan, C., Pillai, V. G., and Ayyar, M. A. S. 1933a. *Indian J. Agr. Sci.* **3,** 589–594.

Ayyangar, G. N. R., Vijiaraghavan, C., Ayyar, M. A. S., and Rao, V. P. 1933b. *Indian J. Agr. Sci.* **3,** 594–604.

Ayyangar, G. N. R., Vijiaraghavan, C., Ayyar, M. A. S., and Rao, V. P. 1933c. *Indian J. Agr. Sci.* **4,** 96–99.

Ayyangar, G. N. R., Ayyar, M. A. S., and Rao, V. P. 1934a. *Indian J. Agr. Sci.* **4,** 90–95.

Ayyangar, G. N. R., Vijiaraghavan, C., Ayyar, M. A. S., Rao, V. P., and Subramanyam, P. 1934b. *Indian J. Agr. Sci.* **4,** 81–89.

Ayyangar, G. N. R., Ayyar, M. A. S., Rao, V. P., and Nambiar, A. K. 1936a. *Madras Agr. J.* **24,** 247–248.

Ayyangar, G. N. R., Ayyar, S., Rao, V. P., and Nambiar, A. K. 1936b. *Indian J. Agr. Sci.* **6** (Part IV), 938–945.

Ayyangar, G. N. R., Rao, V. P., and Ponnaiya, B. W. X. 1936c. *Current Sci. (India)* **6,** 299, 300.

Ayyangar, G. N. R., Ayyar, M. A. S., and Nambiar, A. K. 1937. *Madras Agr. J.* **25,** 107–118.

Barham, H. N., Wagoner, J. A., Campbell, C. L., and Harclerode, E. H. 1946. *Kansas Agr. Expt. Sta. Tech. Bull.* **61.**

Bartel, A. T. 1949. *Agron. J.* **41,** 147–152.

Bowman, D. H., Martin, J. H., Melchers, L. E., and Parker, J. H. 1937. *J. Agr. Research* **55,** 105–115.

Conner, A. B., and Karper, R. E. 1927. *Texas Agr. Expt. Sta. Bull.* **359.**

Dahms, R. G., Guthrie, W. D., and Sieglinger, J. B. 1951. *What's New in Crops and Soils.* **4,** 24.

Dahms, R. G., Snelling, R. O., and Fenton, F. A. 1936. *J. Econ. Entomol.* **29,** 1147–1153.

Davis, F. F., and Sieglinger, J. B. 1952. *Oklahoma Agr. Expt. Sta. Bull.* **B-384.**

Duara, B. N., and Stebbins, G. L., Jr. 1952. *Genetics* **37,** 369–374.

Franzke, C. J. 1945. *South Dakota Agr. Expt. Sta. Circ.* **57.**

Franzke, C. J., and Ross, J. G. 1952. *J. Heredity* **43,** 106–115.

Garber, E. D. 1950. *Univ. Calif. (Berkeley) Publ. Botany* **23,** 283–362.

Garber R. J., and Atwood, S. S. 1945. *J. Am. Soc. Agron.* **37,** 365–369.

Graham, R. J. D. 1916. *Mem. Dept. Agr. India. Bot. Ser.* **8,** 201–216.
Hadley, H. H. 1953. *Agron. J.* **45,** 139–143.
Hilson, G. R. 1916. *Agri. J. India* **11,** 150–155.
Holland, R. F. 1952. Thesis. Texas Agricultural and Mechanical College, Texas.
Huskins, C. L. 1948. *J. Heredity* **39,** 311–325.
Karper, R. E. 1930. *Texas Agri. Expt. Sta.,* **43rd** *Ann. Rept.,* p. 50.
Karper, R. E. 1932. *Am. Naturalist* **66,** 511–529.
Karper, R. E. 1933. *J. Heredity* **24,** 257–262.
Karper, R. E. 1949. *Agron. J.* **41,** 539.
Karper, R. E., and Conner, A. B. 1919. *J. Am. Soc. Agron.* **11,** 257–259.
Karper, R. E., and Quinby, J. R. 1937. *J. Heredity* **28,** 83–91.
Karper, R. E., and Quinby, J. R. 1946. *J. Am. Soc. Agron.* **38,** 441–453.
Karper, R. E., and Quinby, J. R. 1947a. *J. Heredity* **38,** 211–214.
Karper, R. E., and Quinby, J. R. 1947b. *J. Am. Soc. Agron.* **39,** 937–938.
Karper, R. E., Quinby, J. R., and Jones, D. L. 1934. *Texas Agr. Expt. Sta.* **47th** *Ann. Rept.* p. 65.
Karper, R. E., Quinby, J. R., Jones, D. L., and Dickson, R. E. 1932. *Texas Agr. Expt. Sta. Bull.* **459.**
Karper, R. E., and Stephens, J. C. 1936. *J. Heredity* **27,** 183–194.
Laubscher, F. X. 1945. *Union S. Africa, Dept. Agr. and Forestry, Sci. Bull.* **242.**
Leukel, R. W. 1948. *J. Agr. Research* **77,** 201–222.
Leukel, R. W., Martin, J. H., and Lefebvre, C. L. 1951. *U. S. Dept. Agr. Farmer's Bull.* **1959** (rev.).
Martin, J. H. 1936. U. S. Dept. Agr. Yearbook, 523–560.
Martin, J. H. 1941. U. S. Dept. Agr. Yearbook, 343–347.
Martin, J. H. 1945. *J. Heredity* **35,** 98–106.
Martin, J. H. 1951. *What's New in Crops and Soils* **3,** 20–23.
Martin, J. H. 1953. *Econ. Bot.* **7,** 163–181.
Martin, J. H., and Jenkins, M. T. 1951. U. S. Dept. Agr. Yearbook, pp. 159–162.
Martin, J. H., and McMasters, M. M. 1951. U. S. Dept. Agr. Yearbook, pp. 349–352.
Martin, J. H., and Sieglinger, J. B. 1929. *U. S. Dept. Agr. Tech. Bull.* **131.**
Melchers, L. E. 1940. *Am. J. Botany* **27,** 789–791.
Melchers, L. E., and Lowe, A. E. 1940. *Plant Disease Rept. Suppl.* **126,** 165–175.
Meyer, A. 1886. *Ber. deut. botan. Ges.* **4,** 337–363.
Painter, R. H. 1951. "Insect Resistance in Crop Plants," pp. 328–348. The Macmillan Company, New York.
Quinby, J. R., and Gaines, J. C. 1942. *J. Econ. Entomol.* **35,** 265.
Quinby, J. R., and Karper, R. E. 1945. *J. Am. Soc. Agron.* **37,** 916–936.
Quinby, J. R., and Karper, R. E. 1946. *Am. J. Botany* **33,** 716–721.
Quinby, J. R., and Karper, R. E. 1947. *J. Agr. Research* **75,** 295–300.
Quinby, J. R., and Karper, R. E. 1948. *J. Am. Soc. Agron.* **40,** 255–259.
Quinby, J. R., and Karper, R. E. 1949. *Agron. J.* **41,** 118–122.
Quinby, J. R., and Karper, R. E. 1954. *Agron. J.* **46,** 211–216.
Quinby, J. R., Stephens, J. C., Karper, R. E., and Jones, D. L. 1934. *Texas Agr. Expt. Bull.* **496.**
Shedd, C. K., and Walkden, H. H. 1947. *U. S. Dept. Agr. Circ.* **760.**
Sieglinger, J. B. 1924. *J. Agr. Research* **27,** 53–64.
Sieglinger, J. B. 1932. *J. Agr. Research* **44,** 13–20.
Snelling, R. O., Painter, R. H., Parker, J. H., and Osborn, W. M. 1937. *U. S. Dept. Agr. Tech. Bull.* **585.**

Snowden, J. D. 1936. "The Cultivated Races of Sorghum," p. 247. Adlard and Sons, Ltd., London.

Sorenson, J. W., Smith, H. P., Hollingsworth, J. P., and Hontfort, P. T. 1949. *Texas Agr. Expt. Sta. Bull.* **710.**

Stephens, J. C. 1937. *J. Am. Soc. Agron.* **26,** 690–696.

Stephens, J. C. 1944. *J. Am. Soc. Agron.* **36,** 469–470.

Stephens, J. C. 1946. *J. Am. Soc. Agron.* **38,** 340–342.

Stephens, J. C. 1947. *J. Am. Soc. Agron.* **39,** 784–790.

Stephens, J. C. 1951. *Agron. J.* **43,** 382–386.

Stephens, J. C., and Holland, R. F. 1954. *Agron. J.* **46,** 20–23.

Stephens, J. C., Kuykendall, G. H., and George, D. W. 1952. *Agron. J.* **44,** 369–373.

Stephens, J. C., and Quinby, J. R. 1933. *J. Am. Soc. Agron.* **25,** 233–234.

Stephens, J. C., and Quinby, J. R. 1934. *J. Agr. Research* **49,** 123–136.

Stephens, J. C., and Quinby, J. R. 1938. *J. Agr. Research* **57,** 747–757.

Stephens, J. C., and Quinby, J. R. 1939. *J. Agr. Research* **59,** 725–730.

Stephens, J. C., and Quinby, J. R. 1945. *J. Agr. Research* **70,** 209–218.

Stephens, J. C., and Quinby, J. R. 1952. *Agron. J.* **44,** 231–233.

Swanson, A. F. 1928. *J. Agr. Research* **37,** 577–588.

Swanson, A. F. 1951. U. S. Dept. Agr. Yearbook, pp. 353–356.

Swanson, A. F., and Laude, H. H. 1942. *Kansas Agr. Expt. Sta. Bull.* **304.**

Swanson, A. F., and Parker, J. H. 1931. *J. Heredity* **22,** 51–56.

Tullis, E. C. 1951. *Phytopathology* **41,** 529–535.

Vinall, H. N. 1926. *J. Heredity* **27,** 297–299.

Vinall, H. N., and Cron, A. B. 1921. *J. Heredity* **12,** 435–443.

Vinall, H. N., Getty, R. E., and Cron, A. B. 1924. *U. S. Dept. Agr. Dept. Bull.* **1260.**

Vinall, H. N., Stephens, J. C., and Martin, J. H. 1936. *U. S. Dept. Agr. Tech. Bull.* **506.**

Wagner, F. A. 1936. *J. Am. Soc. Agron.* **28,** 643–654.

Wenholz, H. 1934. *N. S. Wales Dept. Agr. Sci. Bull.* **No. 45,** p. 58.

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